ASPECTS OF COASTAL FYNBOS PHENOLOGY

BY

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September 1983

Submitted in partial fulfilment of the requirements for an

MSc Degree

in the Botany Department, Faculty of Science, University of Cape Town

TABLE OF CONTENTS

LIST OF FIGURES AND PLATES

LIST OF TABLES

ACKNOWLEDGEMENTS

I would like to thank:

My supervisor Eugene Moll as much for cheerful support as for his formal supervision of this project.

The CSIR Fynbos Biome Project for financial support.

Charlie Boucher for advice on the selection of study species.

Lampies Lambrechts for explaining the Pella soils to me.

Les Underhill and Patrick Hurly for help with statistical and computer techniques.

All those who gave me access to their unpublished data.

Gary Brown, Frank Coley, Sharon Jongens-Roberts and Willy Stock, not only for sharing your ideas, laboratory space and equipment, but also for all your humour and support.

Margie and Nigel Jarman who did much to organise and encourage.

Timm Hoffmann and Carolyn Stern for measuring Leucospermum plants, under foul conditions

Jim Kaiser and Ken Turner for taking and printing photographs at short notice.

Wendy Metelerkamp for the Thamnocortus drawing.

Gay Perez and Judith Lancaster for drawing the figures.

Mr and Mrs S. Jarman for typing and proof-reading this manuscript.

Geoff Bailey, whose dear dog was my companion throughout the fieldwork.

Finally, I am very grateful to all those who just kept on hoping that I'd finally write an MSc., but even more so to those who knew that I would.

J. E. M. S. September 1983

SUMMARY

This thesis comprises three papers on different aspects of the phenology of several south western Cape coastal fynbos species, with a general introduction and conclusion linking the three. The introduction discusses factors relating to the occurrence of summer growth in some Australian heath and Cape fynbos species.

The first paper deals with the responses of the stem xylem pressure potential of two species to seasonal moisture changes in three soils. The results show that L. parile experienced little or no water stress throughout the investigation. The decreasing spring-summer potentials measured in T. punctatus suggest considerable water stress in this species. The observed differences can be explained in terms of species rooting depth and soil water-holding capacity.

The second paper investigates patterns of seasonal shoot or culm growth in 11 species, in relation to past and present climatic factors and seasonal nutrient availability. The results show that other factors such as root depth and extent, plant age and water-use, and soil water-holding capacity affect the timing of shoot or culm growth in some species.

In the final paper the seasonality of reproductive activity is discussed in relation to the seasonality of vegetative growth and to biotic and abiotic environmental factors. Reproductive activity appears to have little effect on the growth of individual shoots or culms. More research is needed to determine the effects of biotic pollinators, dispersers and predators as well as temperature, photoperiod and soil moisture,on the seasonality of reproductive activity.

In the conclusions summer growth is discussed in relation to water stress, seasonal availability of nutrients and to plant characteristics such as root depth and age.

INTRODUCTION

Phenology has been defined as "the study of the timing of recurring biological events, the causes of their timing with regard to biotic and abiotic forces and the interrelation among phases of the same or different species" (Lieth, 1974). This thesis comprises three papers dealing with various aspects of the phenology of several south western Cape coastal fynbos species. The first investigates the responses of plant water potential in two species, to seasonal changes in moisture in three different soils. The second deals with the seasonality of shoot or culm elongation in eleven species, in relation to both abiotic environmental factors and characteristics of the species. The final paper deals with the seasonality of reproductive phenophases in nine species, in relation to vegetative growth in the same species as well as to biotic and abiotic environmental factors.

The original aim of this research was to investigate the occurrence of the summer growth observed in a coastal fynbos community in the south western Cape (Sommerville in Siegfried, 1982). Summer growth may be related to past climate; a relationship which is difficult to test, and to water- and nutrient-availability which have been investigated here.

Late spring-summer growth in dominant overstorey species in southern Australian heath and some south western Cape species contrasts with the predominance of spring and/or autumn growth in mediterranean-type communities in California, Chile and the Mediterranean basin (Specht and Rayson 1957, Specht 1969, Cody and Mooney 1978, Kummerow 1983).

The summer growth of some southern Australian heath and Cape fynbos taxa has been attributed to their origin in a tropical climate with summer rainfall (Specht and Rayson 1957, Levyns 1964). However there are many different theories regarding the climate, time and place of origin of mediterranean-type taxa. It appears that elements of the sclerophyllous vegetation of the Cape, southern Australia, California and the Mediterranean basin originated, evolved and became widespread under tropical, sub-tropical and temperate conditions during the late Cretaceous to Tertiary period (Specht and Rayson 1957, Burbidge 1960, Cutler 1972, Axelrod 1973, Raven and Axelrod 1974, Axelrod and Raven 1978, Goldblatt 1978, Westman 1978).

The general consensus is that the climate was more humid, with more summer rainfall and less extreme temperatures than under the present mediterranean-type climate. But it is difficult to determine the time, place and therefore climate of origin of specific taxa; "which of these areas represent the individual source for the various groups is a difficult question, and the place of origin of such taxa as Ericoideae or Proteaceae may never be known with certainty" (Axelrod and Raven, 1978). It is therefore virtually impossible to determine whether those species which grow in summer evolved this rhythm in a humid past climate as a result of either generally higher temperatures during the late Tertiary (Specht and Rayson, 1957), or of lower temperatures during the late Cretaceous which limited growth to the warmer summer period (Westman, 1978).

It has been suggested that summer growth is "out-of-phase" with or "ill-adapted" to the present mediterranean climate (Specht and Rayson 1957, Levyns 1964, Kruger 1981). This assumes plant moisture-stress in summer growing species during late spring-summer; the first paper investigates this assumption in two coastal fynbos species with different rooting depths and growth seasons. It is my contention that if growth occurs during the driest season then moisture cannot be the factor limiting growth in these species.

The summer growth peak in fynbos communities on strongly leached soils contrasts with the spring and/or autumn peak in non-fynbos communities on moderately leached soils (Specht et al. 1983). The fact that all these communities occur in the south western Cape under the same meso-climate suggests that certain characteristics of fynbos communities may be related to nutrients rather than climate. Although Aschmann (1973) defines Mediterranean and chaparral ecosystems in terms of climate and Levyns (1964) considers water requirement the main factor separating the Cape Flora from its contiguous Temperate Forest and Succulent Karroo Floras, several authors have pointed out that the Cape Flora both extends beyond and falls short of the limits of the mediterranean-type climate (Marloth 1929, Goldblatt 1978, Kruger 1979). It seems rather that the Cape Flora is more closely associated with infertile soils (Goldblatt 1978, Cowling, in prep.). The most characteristic element of the fynbos: the Restionaceae (Taylor, 1978) is also typically associated with infertile soils (Cutler, 1972).

Studies on the effects of phosphorus-and/or nitrogen-based fertilisers on chaparral and Australian heath species suggest that growth is limited by these nutrients (Specht 1963, McMaster et al. 1982, Schlesinger et al. 1982).

The third paper investigates the phenology of reproductive activity, and in particular its overlap with shoot growth. Because both require nutrients one might assume that reproduction and growth would be asynchronous in a nutrient-limited situation. The observed differences in the growth seasons of mediterranean-type communities have been linked with differences in the soil nutrient status of these communities (Specht et al., 1983). The summer growth of overstorey species in southern Australian heath and Cape fynbos communities was explained in terms of the low nutrient status of these soils. (Specht and Rayson, 1957, Specht 1969, Cody and Mooney 1978). Late spring-summer growth follows the spring release of nutrients from decomposing litter and the withdrawal of nutrients from senescent leaves prior to leaf fall during summer (Specht et al., 1983). The second paper sets out to test this hypothesis in coastal fynbos.

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SEASONAL XYLEM PRESSURE POTENTIALS IN TWO SOUTH AFRICAN COASTAL FYNBOS SPECIES ON THREE SOILS

J.E.M.Sommerville and E.J.Moll

SUMMARY

The seasonal dawn and midday stem xylem pressure potentials of two South African coastal fynbos species, Thamnocortus punctatus and Leucospermum parile, were measured on three soil forms from July 1981 to May 1982. The results show that the response of the two species was markedly different; the deeper rooted L. parile exhibited little or no moisture stress throughout the year while the decreasing spring-summer (September-March) potentials of the shallow rooted T. punctatus suggest considerable water stress. The potentials of L. parile are high by comparison with those for other mediterranean shrubs but both rainfall and shoot growth data suggest that the summer-drought period studied was not extreme. L. parile appears to conform to Specht's (1972) concept of a water-conservative, mediterranean, evergreen sclerophyll. J.M. Miller et al. (pers. comm.) suggest that restioids, including T. punctatus, employ a "Boom or Bust" water strategy, using a lot of water when it is available and conserving it when it is scarce; these data support this concept. In terms of soil type the observed differences in the xylem potentials of both species can be explained by differences in soil water-holding capacity.

SEASONAL XYLEM PRESSURE POTENTIALS IN TWO SOUTH AFRICAN COASTAL FYNBOS SPECIES ON THREE SOILS

INTRODUCTION

A mediterranean climate as experienced at the study area in the S W Cape region of South Africa, characteristically includes some degree of summer drought (Schulze and McGee 1978). The present study set out to investigate the response of the stem xylem pressure potential of two species with different rooting depths to the summer period of assumed moisture stress (Kruger 1979). Several authors have noted that Californian and Chilean mediterranean shrubs with deeper root systems experience less water stress, evidenced by higher xylem potentials, than shallow rooted shrubs do (Morrow and Mooney 1974, Poole and Miller 1975, Riveros et al. 1976, Krause and Kummerow 1977, Burk 1978, Giliberto and Estay 1978, Schlesinger and Gill 1980, Roberts et al. 1981, Miller 1982). More specifically, Roberts (1982) reports a 1 to 1.5 MPa reduction in the water potential of Quercus agrifolia on the removal of 70% of the lateral roots. In Australian heath communities Groves and Specht (1965) found that roots were deeper in dry than in wet soils and that community water relations were affected by root depth (Specht and Jones 1971). However Hanes (1965) found that the shallow-rooted Californian redshank appeared to be less water-stressed and grew during spring to summer, in comparison with the deeper-rooted chamise, which grew in late winter to spring.

A further aim of this study was to investigate the effects of soil type on the xylem pressure potential of the species. Barnes and Tyrone Harrison (1982) found marked differences in the seasonal distribution and availability of moisture in the coarse upper dune sands and finer lowland soils of the Nebraska sandhills. In comparison with the finer soils there was more moisture available throughout the sandy profile during the dry summer-autumn period. In the finer soils, on the other hand, more moisture was available near the surface during the wet winter-spring period.

Study Areas

The study areas were at Pella, the coastal fynbos intensive study site for the CSIR Fynbos Biome Project, located 35 km NE of Cape Town at 33° 31' S 18° 32.5' E. The vegetation is dominated by evergreen, sclerophyllous species representing the three characteristic fynbos elements: the proteoid, ericoid and restioid (Taylor 1978, Kruger 1979). The study areas were situated in five-year-old Leucospermum parile-Stoebe leucocephala, L. parile-Thamnocortus punctatus and Diastella proteoides-Berzelia abrotanoides communities (Boucher and Shepherd pers. comm.). Figure 1 illustrates the monthly rainfall and absolute maximum and minimum air temperatures from June 1981 - May 1982, collected at the Pella weather station. The rainfall data are compared with the 49-year average from the nearest Weather Bureau Station, at Burgherspost (33° 30' S 18° 32' E). The soils at Pella are aeolian sands, a catena of five freely-draining soils exists, with two seasonally-waterlogged soils completing the seven major types (Fry, pers.comm.).The soil forms investigated were the Hutton, Clovelly and Westleigh (MacVicar et al. 1977). The Hutton soil at the head of the catena is a well-drained, red, medium sand with a high iron content which is usually associated with a relatively high water-holding capacity (J.J.N. Lambrechts, pers. comm.). The Clovelly is intermediate on the catena, a yellow, medium sand with an intermediate iron content and water-holding capacity. The Westleigh is a grey, slightly coarser medium sand which exhibits soft, plinthic mottling within 30 cm of the surface, indicating that waterlogging has occurred in the past.

Study Species

The two species studied, Leucospermum parile (Salisb. ex Knight) Sweet and Thamnocortus punctatus Pillans, were selected because of their widespread abundance at the study site and the consequent concentration of plant-nutrient, -litter and -phenology studies on these species. L. parile, a member of the Proteaceae, is an "erect to semi-erect rounded shrub up to 1.5m in height, with a single stout main stem... Leaves... covered with a short dense canescent indumentum of short crisped hairs; ... usually with two to six inflorescences clustered in the axils of the uppermost leaves of the flowering stem." (Rourke 1972). It has an extensive tap root system concentrated in the upper 40 cm but extending to below 2 m (S. Jongens pers. comm.). Thamnocortus punctatus belongs to the most characteristic fynbos family (Taylor 1978), the Restionaceae, ".. a very old Southern Hemisphere family found chiefly in South Africa and Australia." (Levyns 1966). The Restionaceae are usually dioecious, perennial

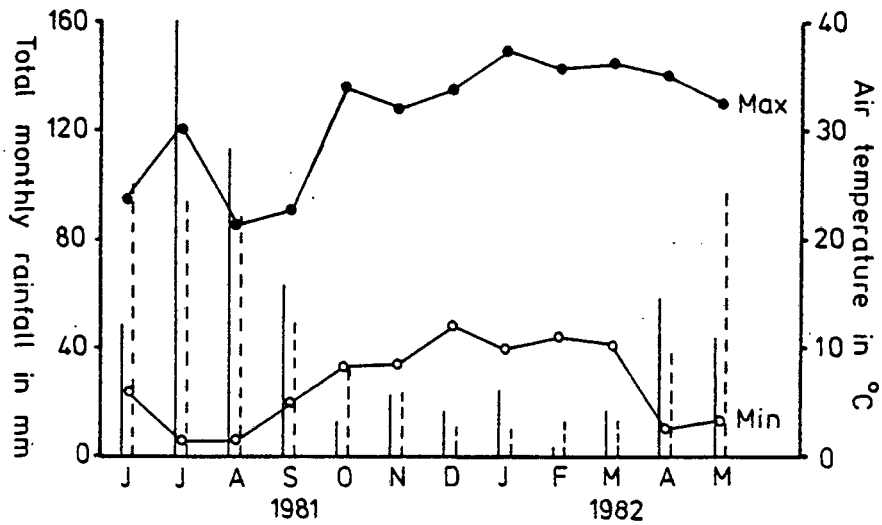

Figure 1 Monthly rainfall (|) and maximum (●——●) and minimum air temperatures (○— —○) at the Pella climate station during the study period. 49-year mean monthly rainfall from Burgherspost (¦).

rush- or sedge-like, evergreen hemicryptophytes with photosynthetic stems and the leaves reduced to papery sheaths at the nodes, some species have finely divided barren branches made up of both stem and leaf material (J. Hardcastle pers. comm.). T. punctatus (Figure 2) has caespitose, erect, simple stems, some of which bear barren branches; the male spikelets are numerous and in lax, panicled cymes 1.2 - 2 cm long (Pillans 1928). The male plants sampled were 70 - 80 cm in height with densely branched rhizomes and shallow, fibrous root systems concentrated in the upper 10 cm of the soil (Sommerville and Stock pers. obs.).

Shoot Xylem Potential

Xylem potentials were measured using the pressure chamber technique (Scholander et al. 1965). These measurements are assumed to approximate closely the total xylem water potential since the solute and matric components of water potential are constant or negligible in most non-halophytic plants (Boyer 1969, Kappen et al. 1972). Measurements were made on at least two of the current year's shoots on a single individual of both L. parile and T. punctatus, the number being increased to provide a more representative range when high variability was encountered in the readings. At the same time the number was limited to reduce the time elapsed between readings on the three soil types. Plant size, shoot age and height were comparable throughout the investigation, thus avoiding these sources of variation (Waring and Cleary 1967, Ritchie and Hinckley 1975). The time elapsed between cutting and measuring xylem pressure of a shoot was kept to a minimum while the rate of increase of air pressure was kept relatively constant in order to reduce errors due to these factors (Waring and Cleary 1967, Ritchie and Hinckley 1975). Measurements were made as close to civil dawn and midday as possible to compare the plants' responses to soil moisture and evaporative stress respectively (Oberbauer and Billings 1981). Measurements were made at approximately monthly intervals from July 1981 on L. parile and from September 1981 on T. punctatus, once the shoots were long enough to be measured, and continued until May 1982.

Figure 2 Sketch of part of a 6-year-old male Thamnocortus punctatus plant.

a) fibrous roots
b) rhizome
c) photosynthetic culm
d) papery leaf sheath
e) barren branch
f) mature inflorescence

Soil Moisture

Gravimetric determinations of soil moisture were carried out on soil samples collected with a soil-corer at depths of 0-5, 15, 40 and 80 cm in each soil type. Four replicates were collected at each depth on each sampling date. Soil water potential and temperature were measured using Wescor psychrometers buried at 0-5, 15, 40, 80 and 100 or 150 cm in each soil type. The psychrometers proved rather unreliable, particularly those at 0-5 cm, presumably because of high temperatures; psychrometers measure vapour pressure, whose relationship with soil moisture is extremely temperature-sensitive (Brown 1970). Several other factors which may account for this unreliability include contamination of the psychrometers, incorrect temperature correction of the readings and insufficient psychrometer equilibration time (Savage et al. 1979).

Veihmeyer and Hendrickson (1950) question the reliability both of measurements made from soil samples and from instruments buried in the soil because the absorbing portions of plant roots do not always thoroughly permeate the soil. They advocate the use of the predawn maximum xylem potential as an approximation of "effective soil moisture". But, as soil moisture availability decreases and daily evaporative stress increases, plant equilibration time increases so that plant predawn potential diverges from soil moisture availability (Ritchie and Hinckley 1975).

RESULTS

In L. parile, dawn potentials on all three soils, presented in Figures 3a, b and c, were high and relatively constant. There was a slight increase during winter-spring; from July-August (-0.17 to -0.32 MPa) to October (-0.02 to -0.32 MPa). This was followed by a general decrease from October to February (-0.17 to -0.5 MPa) interrupted in both the Clovelly and Westleigh soils by an increase in the January values. The lower potentials on the Clovelly soil in February (-0.5 $\pm$ 0.03 MPa) were the result of the measurements being made nearly two hours after dawn. Finally the potentials increased during autumn; February to May (0 to -0.05 MPa). The midday potentials were lower and exhibited an overall decrease from July (-0.42 to -0.46 MPa) to February (-0.69 to -0.85 MPa) followed by an increase, which was most marked on the Hutton soil, from February to May (-0.12 to -0.48 MPa), comparable to the trend in the dawn potentials.

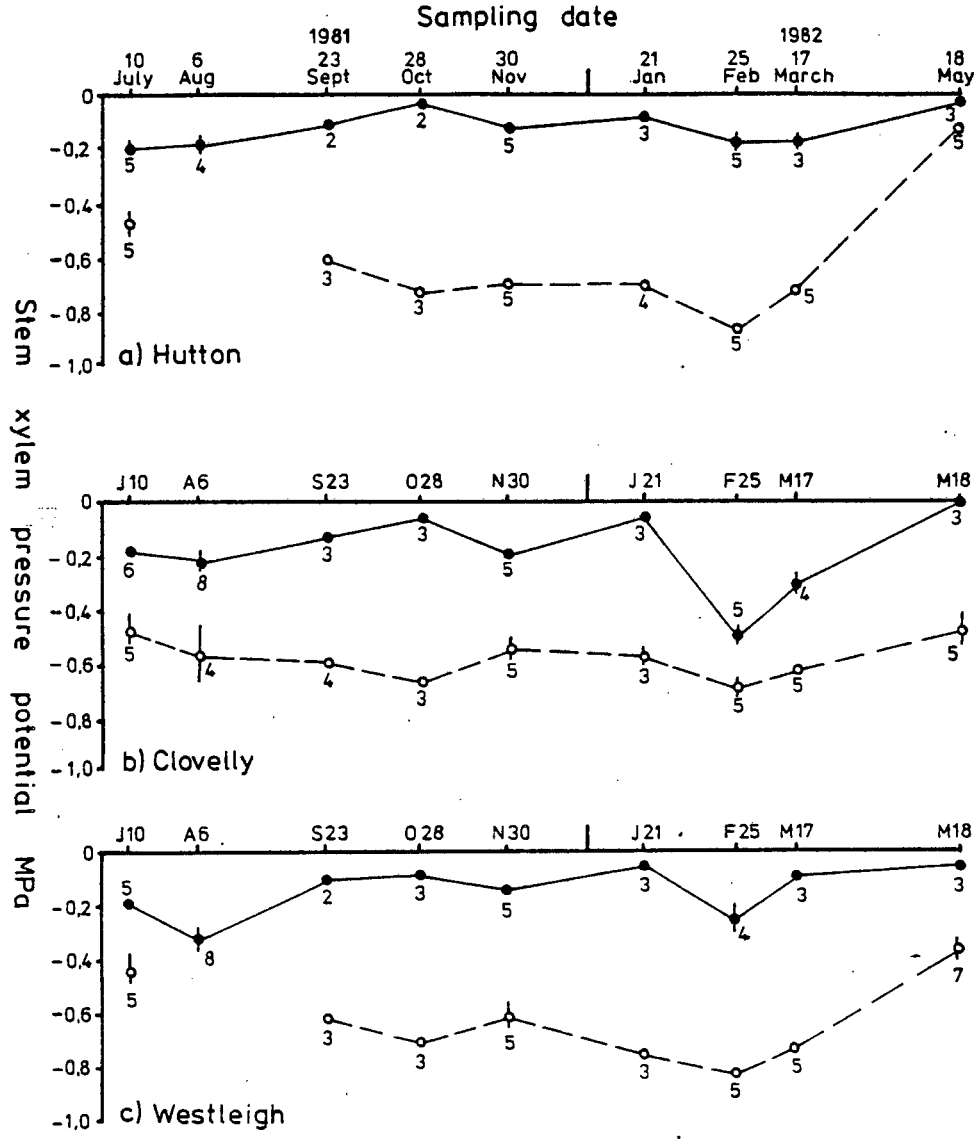

Figure 3 Seasonal dawn (●——●) and midday (○– –○) mean stem xylem pressure potentials of Leucospermum parile on the Hutton (a), Clovelly (b) and Westleigh (c) soil-types (sample size indicated above).

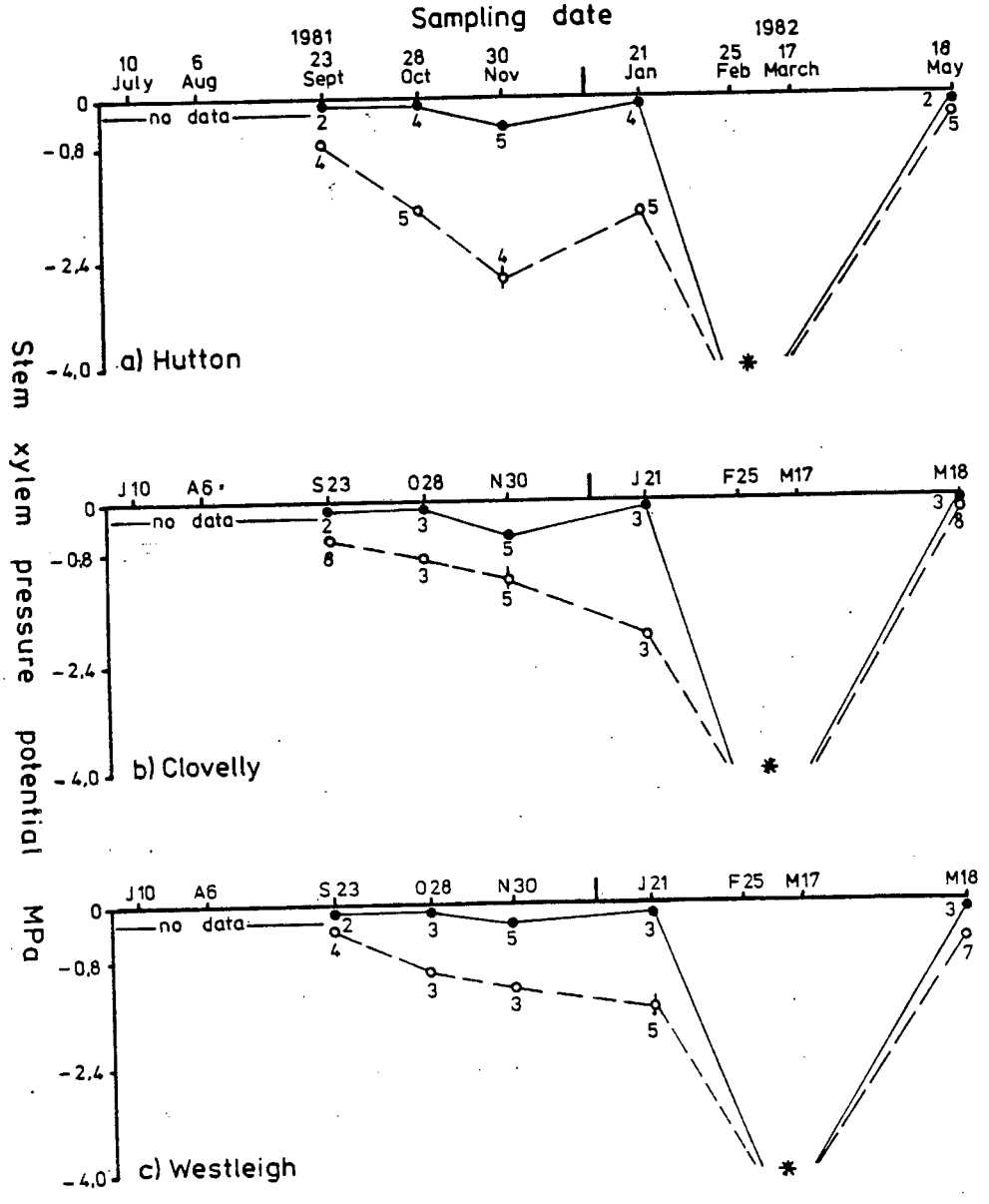

Figure 4 Seasonal dawn (●——●) and midday (○– – –○) mean stem xylem pressure potentials of Thamnocortus punctatus on the Hutton (a), Clovelly (b) and Westleigh (c) soil-types (sample size indicated above).

✱ 4 MPa pressure gauge limit.

There was an overall decrease in T. punctatus dawn potentials (Figure 4) during spring and summer: from September (-0.1 to -0.13 MPa) to February and March (below the -4 MPa limit of the pressure gauge). As in L. parile this decrease was interrupted on all three soil types by higher potentials in January. Potentials increased dramatically from March to May (-0.03 to -0.17 MPa). Midday potentials were lower but exhibited similar trends to the dawn potentials, although the increase in the January potentials was less marked in both the Clovelly and the Westleigh soils. In addition, midday potentials decreased more rapidly on the Hutton than on either the Clovelly or the Westleigh soils.

The gravimetric soil moisture data (Figure 5) illustrated the progressive drying-out of all three soils from August to March and their rehydration by May. The increase in moisture in the surface layers in January was more marked in the Hutton than in either the Clovelly or the Westleigh soil. The soil temperature data (Figure 6) show slight increases from November to February and decreases from February to May, which are most marked in the upper soil surface.

DISCUSSION

The seasonal xylem pressure responses of the two species was markedly different. The magnitude and relative constancy of the deeper-rooted L. parile xylem potentials throughout the study period suggest little or none of the assumed summer water stress. The moderate leaf conductances and xylem potentials measured by J.M. Miller et al. (pers. comm.) on L. parile in November and December 1981 support this. L. parile potentials may be compared with those of three species of Rhus from Californian chaparral which were -1 MPa at dawn and the daily minimum not less than -2 MPa throughout the year (Poole and Miller 1981). Two Chilean matorral species, Lithraea caustica and Quillaja saponaria, exhibited minimum values of greater than -2.5 MPa (Giliberto and Estay 1978). But these potentials are lower than the 0 to -0.32 MPa dawn and -0.12 to -0.86 MPa midday potentials we recorded for L. parile. The highest xylem potentials we have seen quoted for mediterranean, evergreen shrubs were -0.5 MPa at dawn and a minimum of -2 MPa for Ceanothus velutinus and Arctostaphylus patula in montane chaparral (Conard and Radosevich 1981). However it is obvious from the literature that xylem pressure potentials can vary tremendously with severity of drought, for example Parsons et al. (1981) data for Arctostaphylus viscida. A comparison of the rainfall during the study period with the 49-year mean (Figure 1) shows that there was above

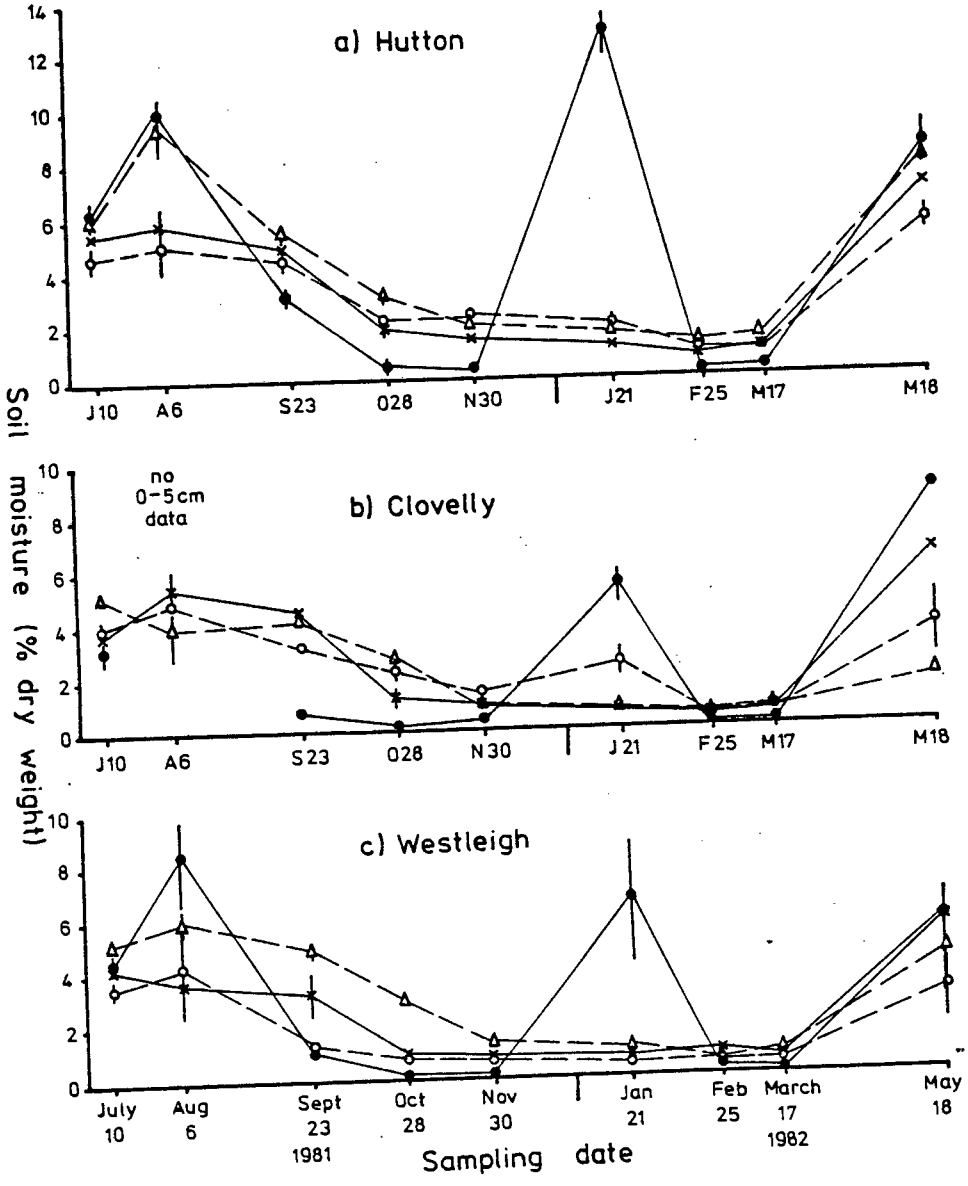

Figure 5 Seasonal gravimetric soil moisture content of the Hutton (a), Clovelly (b) and Westleigh (c) at 0-5 cm (●——●), 15 cm (○– –○), 40 cm (×——×) and 80 cm (Δ– –Δ), mean of 4 samples ± std. error.

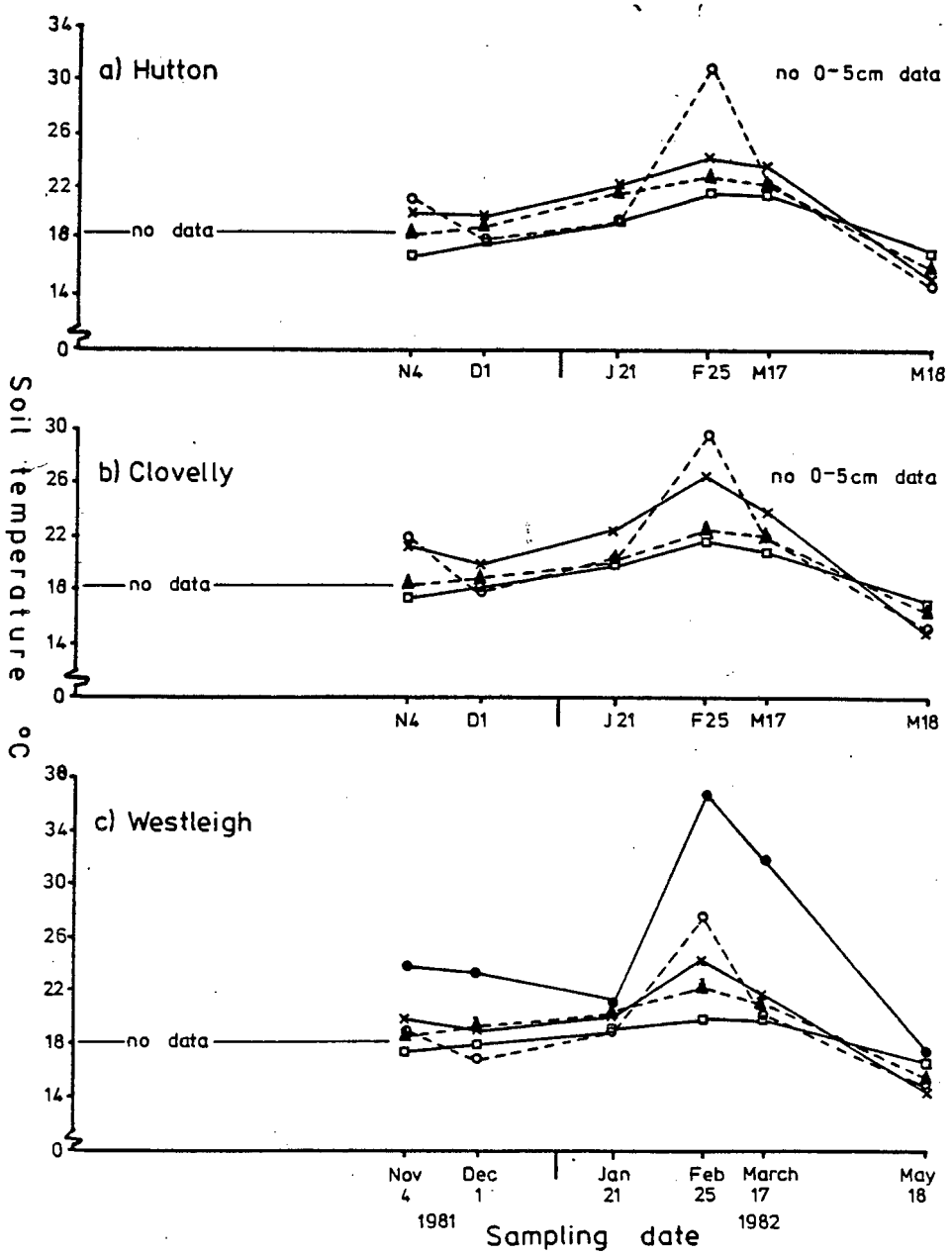

Figure 6 November 1981 to May 1982 soil temperatures in the Hutton (a), Clovelly (b) and Westleigh (c) at 0-5 cm (•—•), 15 cm (o—o), 40 cm (×—×), 80 cm (▲—▲) and 100 or 150 cm (□—□), mean of 4 samples ± std. error.

average winter (July and August) and mid-summer (January) rainfall, suggesting that the 1981-1982 drought was not severe and accounting for the high potentials in L. parile. The similarity between the timing of L. parile shoot growth on the three soils during 1981-1982, by comparison with the significant differences in 1980-1981, is consistent with this (Sommerville pers. obs.).

T. punctatus, with its shallow root system, exhibited considerable moisture stress as evidenced by the low potentials observed in February and March. The decrease in dawn and midday xylem potentials from September to February and March corresponds to a decrease in gravimetric soil moisture. The increases observed in January may be attributed to the unusually high rainfall that month (Figure 1) with 6.9 mm falling on the sampling day and 9 mm the day before. The September to January dawn potentials remained relatively high, suggesting that during this period the plants were able to equilibrate overnight from the increasing daytime stress. But in February and March both the midday and, more markedly, the dawn potentials decreased dramatically from -0.15 MPa to less than -4 MPa, there was obviously little or no overnight equilibration. This dramatic decrease in xylem potential is not paralleled by air temperatures (Figure 1), soil moisture (Figure 5) or the values measured on L. parile (Figure 3). A study of the seasonal changes in above- and below-ground phytomass of T. punctatus showed that the young roots formed during winter-spring had shed their absorptive cortex by summer (Sommerville and Stock pers. obs.). Presumably above a certain level of moisture stress during summer the cortex is shed, probably rendering the roots non-absorbent. This could account for the sudden decrease in both dawn and midday xylem potentials. An investigation of another species of Restionaceae at Pella, Cannamois acuminata, showed that a thick cuticle develops on the culms at the same time that the root cortex sloughs off under conditions of water stress (J. Hardcastle pers. comm.). If this thick cuticle develops in T. punctatus the low pressure potentials may be a measure of the resistance of the culms to gas exchange rather than a measure of xylem potential. The growth of new absorptive roots combined with increased soil moisture accounts for the high potentials measured in May (Sommerville and Stock pers. obs.).

Unfortunately midday xylem potentials for T. punctatus cannot be directly compared with those for species in other mediterranean regions because of the limits of our pressure gauge and the lack of data for comparable growth forms. J.M. Miller et al. (pers. comm.) have comparable data for T. punctatus at Pella in November and December. Their data for other restioids are rather variable, which they attribute to differences in root depth and phenology. With reference to the low dawn potentials in T. punctatus several species of mediterranean shrub have exhibited some overnight recovery from minimum potentials of less than -4 MPa (Poole and Miller 1975, 1981, Burk 1978, Baker et al. 1982). Cryptocarya alba, on the other hand, showed little or no recovery from potentials of only -3,4 MPa (Riveros et al. 1976).

One of the most obvious differences between L. parile and T. punctatus, which may account for the differences in xylem potential and implied water stress, is the depth and extent of their root systems. Our data agree with those for many other mediterranean shrub species, with the deeper rooted L. parile exhibiting higher xylem potentials than the shallow rooted T. punctatus. However it is unlikely that xylem pressure potential is controlled by a single factor such as root depth and two other major areas of influence are identified in the literature. Leaf orientation, size and anatomy affect xylem pressure by their influence on leaf exposure, temperature and water loss (Mooney and Kummerow 1971, Harrison et al. 1974, Morrow and Mooney 1974, Riveros et al. 1976, Burk 1978). The photosynthetic organs of the two species studied are very different; L. parile has leaves with a dense layer of surface hairs which probably reduce water loss, T. punctatus, on the other hand, photosynthesises largely through erect, cylindrical culms which are probably less exposed to sunlight; they also have deeply sunken stomata (J. Hardcastle pers. comm.). Secondly, the physiological control of transpiration, photosynthesis and stomatal closure affects xylem potential (Hanes 1965, Harrison et al. 1974, Riveros et al. 1976, Ng and Miller 1980, Poole and Miller 1981). No data are available on the physiological responses of L. parile and T. punctatus and in particular on their tolerance of low xylem potentials, a feature which Ritchie and Hinckley (1975) emphasise as an important constraint on direct comparisons of species water stress based on xylem pressure potentials.

Although the gravimetric soil moisture data show few marked, consistent differences between soils, plant-available moisture levels were probably considerably different. The high water-holding capacity normally associated with the high iron content and small particle size characteristic of Hutton soils would make plant-available moisture levels lower than those of the coarser-grained, lower iron-containing Clovelly and Westleigh soils. There were some isolated differences in the responses of both species on the three soils. The increases in the January dawn potentials of L. parile on both the Clovelly and the Westleigh soils were not observed on the Hutton soil. This may be explained by the assumed higher water-holding capacity of the Hutton, as evidenced by the soil moisture data (Figure 5a), the increase due to the rain on and prior to the sampling date was confined to the 0-5 cm layer so that little moisture percolated through to the L. parile roots deeper down. The lower moisture contents of the upper 5 cm in both the Clovelly and the Westleigh soils and the increase in the 15 cm Clovelly samples suggest that the rain had percolated deeper in these soil types. We have no evidence to explain the slightly lower midday potentials throughout most of the year on both the Hutton and the Westleigh soils, nor for the appreciably lower potentials on the Hutton soil in May.

Midday T. punctatus potentials on the Hutton differed from those on both the Clovelly and the Westleigh soils during the September-January period (Figure 4). Firstly, the Hutton potentials decreased more rapidly, presumably as a consequence of the higher water-holding capacity of this soil as discussed above. Further, the increase observed in the January potentials was most marked on the Hutton soil, probably because there was more water retained in the 0-5 cm layer (Figure 5) and because T. punctatus roots are largely confined to the 0-10 cm layer (Sommerville and Stock pers. obs.).

CONCLUSIONS

From these data it appears that L. parile did not experience the assumed summer moisture stress (Kruger 1979) while T. punctatus exhibited increasing moisture stress during spring and summer. This difference in response may be explained in terms of differences in rooting depth and extent, photosynthetic organs and/or physiological response.

Californian chaparral has been divided into: dry areas receiving less than 500 mm rainfall per annum with a predominance of species with high leaf conductances, variable seasonal water potentials, shallow roots and seed-regeneration. The wetter areas receive more than 500 mm rain and their species have lower leaf conductances, relatively constant water potentials, deep roots and regeneration from the rootstock (Miller 1981). T. punctatus exhibited moderate leaf conductances (J.M. Miller et al. pers. comm.) but otherwise conformed to the description of a dry area species. L. parile exhibited moderate leaf conductances and seed-regeneration in combination with stable water potentials and deep roots so that it does not completely fit either the wet or the dry species description, which is not surprising considering that the Burghers-post 49-year rainfall mean is 555 mm. From this study and data on leaf conductance and stem xylem potential (J.M. Miller et al. pers. comm.) it appears that proteoids, including L. parile, conform more closely to Specht's (1972) concept of a water-conservative mediterranean shrub with high, constant seasonal xylem potentials, moderate leaf conductances and growth continuing through spring to summer. Specht maintains that many Australian species have high temperature requirements for growth due to their tropical origin; for growth to occur during summer these species must use water conservatively. Miller and Poole (1979) argue that conservative water use may be possible in pure stands, but not in mixed stands, due to competition. Data for Adenostoma fasciculatum in pure and mixed stands on different slopes lend some support to their argument (Roberts et al. 1981).

J.M. Miller et al. (pers. comm.) suggest that restioids such as T. punctatus employ a "Boom or Bust" strategy involving high water use when water is abundant and conservative use when water is scarce. This may in turn be related to the shallow rooting depth of these species. The high transpiration rates under non-stressed conditions, contrasted with the formation of a thick stem cuticle layer and the sloughing of the root cortex under conditions of moisture stress in Cannamois acuminata, support this

concept (J. Hardcastle pers. comm.). Differences in soil moisture in the three soils were not as marked as those in the soils of the Nebraska sandhills. It is possible that the methods used for measuring both plant and soil moisture were not sufficiently sensitive and/or sampling was too infrequent to adequately illustrate differences. But from both the high xylem potentials in L. parile and the rainfall data it appears that the 1981-1982 summer drought period was not severe, which would make differences in moisture stress less obvious. The similarity between the timing of L. parile shoot growth on the three soils during the 1981-1982 growth season by comparison with the significant differences in 1980-1981, is consistent with this hypothesis (Sommerville pers. obs.).

ACKNOWLEDGEMENTS

We would like to acknowledge the financial support of the Fynbos Biome Project under the Co-operative Scientific Programme of the CSIR. We would also like to thank J.M. Miller and Dr J.A. Day for their constructive criticisms of preliminary drafts of this manuscript.

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SEASONAL SHOOT OR CULM GROWTH OF ELEVEN SOUTH WESTERN CAPE COASTAL FYNBOS SPECIES

J.E.M. Sommerville

SUMMARY

The monthly elongation of shoots or culms of eleven coastal fynbos species, representing the characteristic restioid, proteoid and ericoid components, was measured from June 1980 to February 1982. In addition the depth and extent of the root system and seasonality of vegetative litter fall were investigated. The data show that the growth of these species occurred predominantly during spring and summer, and that there was no obvious correlation between growth form and growth season. There was no conclusive evidence of causal relationships between seasonal availability of nutrients or climatic factors and growth season. The growth season of some of the species investigated appears to be affected by root depth and extent, soil moisture-holding capacity, plant water-use efficiency and plant age.

SEASONAL SHOOT OR CULM GROWTH OF ELEVEN SOUTH WESTERN CAPE COASTAL FYNBOS SPECIES

INTRODUCTION

This study set out to investigate the seasonality of growth in coastal fynbos species and to attempt to relate the observed growth patterns to factors such as past climate, nutrient cycling and the physical environment.

Specht and Rayson (1957) considered the "summer-growth rhythm instead of the spring growth typical of similar vegetation in other mediterranean-type regions.." an outstanding feature of southern Australian heath. Observations of growth in a south western Cape coastal fynbos community suggested that here too many species grow during summer (Sommerville in Siegfried, 1982). The summer growth observed in some southern Australian heath species has been attributed to their evolution under tropical conditions (Specht and Rayson, 1957). It is almost impossible to test whether past climate affects the current growth season of a taxon because of the difficulties involved in determining the precise time, place and therefore climate of origin (Axelrod and Raven, 1978). Based on fossil evidence and present distribution patterns it seems that members of both the Proteaceae and the Restionaceae, important fynbos families (Taylor 1978, Kruger 1979), may have either tropical (Levyns 1958, Johnson and Briggs 1963, Raven and Axelrod 1974, Goldblatt 1978) or temperate ancestors (Beard 1959, Burbidge 1960, Axelrod and Raven 1978).

Another explanation of summer growth is that "shoot growth in late spring-early summer may be the result of the redistribution of metabolites" within the plant rather than the uptake of nutrients by roots from the soil (Groves, 1965). Studies of nutrient levels in typical mediterranean-type evergreen, sclerophyll species have shown that there is a decrease in the nitrogen and phosphorus content of shoots and leaves with age, suggesting that re-allocation from older to younger parts does occur (Mooney and Rundel 1979, Shaver 1981, Grey 1983).

Several Australian heath species appeared to produce organically bound polyphosphates when fed high levels of phosphate (Jeffrey 1964, 1968). These data led Specht and Groves (1966) to suggest that phosphates were taken up from the soil during spring and stored as polyphosphates (cf Mooney and Rundel, 1979, nutrient uptake during winter in chaparral species). These polyphosphates would be mobilised by hydrolysis during the dry summer period and "species whose growth coincided with the period of hydrolysis would have a decided advantage" (Specht and Groves, 1966). However some doubt exists as to whether polyphosphates are synthesised by higher plants. Jeffrey's method of extracting and measuring polyphosphates has been criticised because it is not specific and includes phosphorus from nucleic acids (Callow et al., 1978).

More recently Specht et al. (1983) have distinguished between the growth of overstorey species (often Proteaceae) and of mid- and ground-stratum species (ericoid sub-shrubs and restioid species) in heathland communities including south western Cape fynbos. Shoot growth of the mid- and ground-stratum species tends to occur in autumn or spring when soil-moisture and temperature conditions are most favourable (Specht et al., 1983). The growth of heathland overstorey species during summer is related to the release of nutrients into the soil from litter decomposing under optimal warm, moist conditions during spring and to the re-distribution of nutrients from senescent leaves prior to leaf fall during late-summer (Specht et al., 1983).

The shoot growth of several chaparral, matorral and southern Australian heath species during spring and/or summer has been related to several environmental factors acting singly or in combination: increasing temperature, decreasing moisture-availability and increasing photoperiod (Adams and Radosevich 1978, Montenegro et al. 1979, Kummerow et al. 1981, Nilsen and Muller 1981, Specht 1981). Hanes (1965) and Pierce (in prep.) both suggest that in addition to environmental factors there are "internal physiological" or "endogenous" rhythms affecting phenophases in chaparral and fynbos species respectively, but neither elaborate or explain how those rhythms operate independently of either physical or biological environmental factors. I have seen no reports of the possible influence of biotic factors such as herbivores and plant pathogens on plant growth season.

The principle of temporal partitioning of resources has been used to explain differences in the timing of phenophases of species in a community. The seasonal spread of the flowering of species in a tropical rainforest was interpreted as a temporal partitioning of the hummingbird-pollinator resource which these species share, reducing interspecific competition (Stiles, 1977). Other authors consider the observed spread in the flowering times of competing species to be random (Rabinowitz et al. 1981, Ranta et al. 1981). But it is no simple matter to statistically test whether the observed spread is random, or as a result of the temporal partitioning of a resource (Cole 1981, Gleeson 1981). Further, as Pierce points out, phenology does not necessarily reflect resource use, for example there may be a lag between nutrient uptake and the resultant shoot growth. The sometimes complex relationships between, often seasonally variable, physical and biological resources make temporal partitioning "virtually untestable" (Pierce, in prep.) and as such it will not be considered further.

STUDY AREAS

The study areas were at Pella, the coastal fynbos intensive study site for the CSIR Fynbos Biome Project, located 35 km NE of Cape Town (33° 31' S 18° 32.5' E). The vegetation is dominated by evergreen, sclerophyllous species representing the three characteristic fynbos elements: the proteoid, ericoid and restioid (Taylor 1978, Kruger 1979). The three study areas were situated in five year old Leucospermum parile-Stoebe leucocephala, L. parile-Thamnocortus punctatus and Diastella proteoides-Berzelia abrotanoides communities (Boucher and Shepherd, in prep.).

The soils at Pella are aeolian sands, a catena of five freely-draining soils exists, with two seasonally water-logged soils completing the seven major types (M. Fry, pers. comm.). The communities investigated were on Hutton, Clovelly and Westleigh soil forms, respectively (MacVicar et al., 1977).

Figures 1 and 2 illustrate climatic data collected during the investigation at Pella, the ATS weather station at Philadelphia (33° 40' S 18° 35' E) and Burgherspost farm (33° 30' S 18° 32' E).

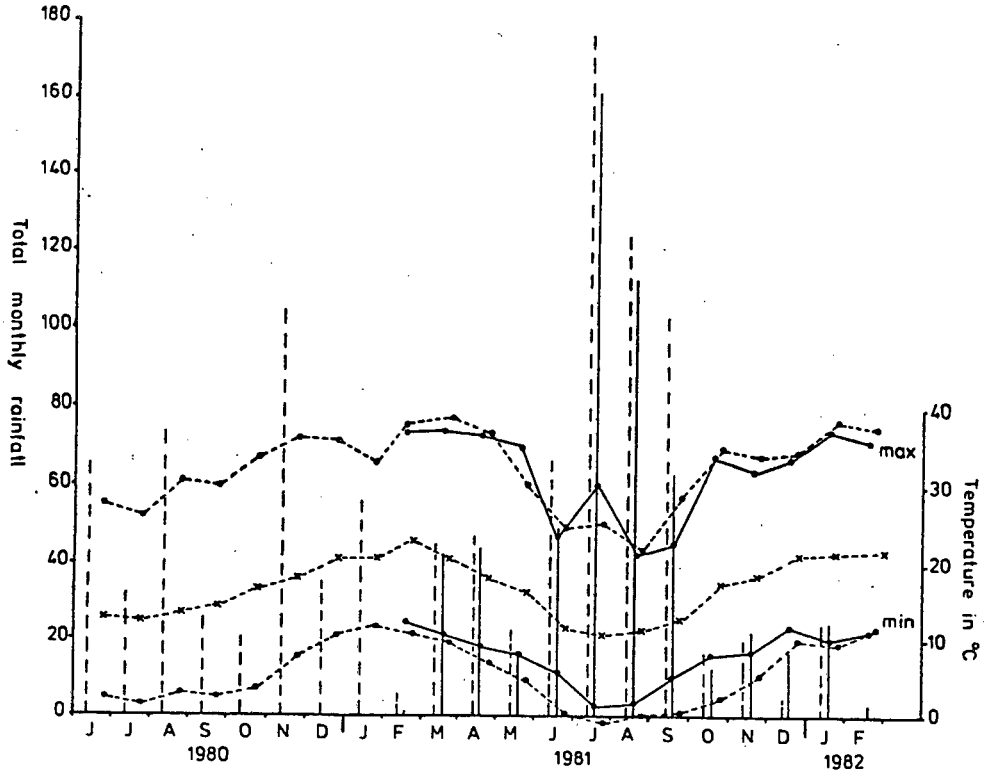


Figure 1 Monthly rainfall and temperature data from June 1980-February 1982. Total monthly rainfall from the Pella climate station (|) and Burgherspost farm (¦). Absolute monthly maximum (●——●) and minimum (●——●) air temperatures from the Pella climate station and maximum (●– – –●), minimum (●– – –●) and average (x– – –x) temperatures from the Philadelphia weather station.

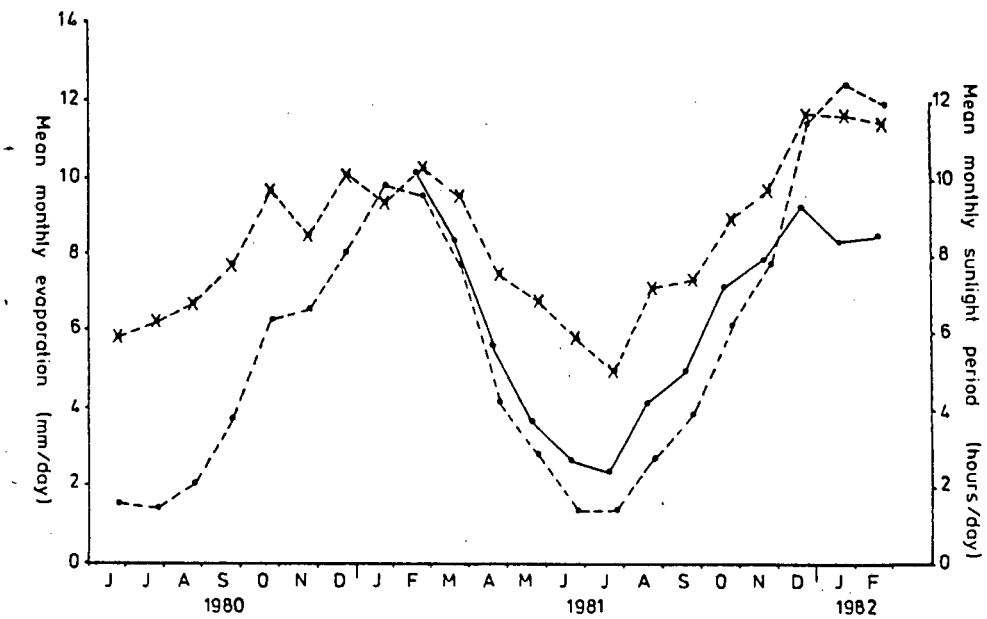


Figure 2 Average monthly A-pan evaporation from the Pella climate station (●——●) and Philadelphia weather station (●– –●), from June 1980 to February 1982. Average monthly sunlight hours (–X–) from the Philadelphia weather station, from June 1980 to February 1982.

METHODS

Five or six common species, including representatives of the characteristic restioid, proteoid and ericoid elements, were investigated at each of the three study areas (Table 1).

TABLE 1 Species investigated at the study areas on the Hutton, Clovelly and Westleigh soil forms

	HUTTON	CLOVELLY	WESTLEIGH
RESTIOID SPECIES			
Thamnocortus punctatus Pillans Fam. Restionaceae	X	X	X
Restio monanthus Mast. Fam. Restionaceae	X		
Staberoha distachya (Rottb.) Kunth Fam. Restionaceae		X	X
PROTEOID SPECIES			
Leucospermum parile (Salisb. ex Knight) Sweet Fam. Proteaceae	X	X	X
Leucadendron lanigerum Buek ex Meisn. var. *lanigerum* Fam. Proteaceae	X		
Diastella proteoides (L.) Druce Fam. Proteaceae			X
Protea burchellii Stapf Fam. Proteaceae	X		
ERICOID SPECIES			
Metalasia muricata (L.) D. Don Fam. Asteraceae		X	X
Staavia radiata (L.) Dahlg. Fam. Bruniaceae	X		
Berzelia abrotanoides (L.) Brongn. Fam. Bruniaceae			X
Grisebachia plumosa Klotzsch subsp. *plumosa* Fam. Ericaceae		X	

Two shoots or restioid culms were labelled on each of ten plants of each species at the three areas. Shoot or culm length was measured at approximately monthly intervals from June 1980 to March 1982. Wherever possible the same shoots were measured throughout, however, some shoots had to be replaced due to death, damage or loss of the label. This was a particular problem in R. monanthus, M. muricata, S. radiata, B. abrotanoides.

T. punctatus produces a new cohort of culms from the rhizome each year, ten culms from each of the 1979, 1980 and 1981 cohort were labelled and measured at each study area. S. distachya, on the other hand, produces new culms spasmodically throughout the year. Since my prime interest was in growing culms, new culms were labelled at various times throughout the first year of the investigation.

Two, 15 cm diameter pots were placed under an individual or group of small individuals of each species at all three sites. These were cleared at approximately monthly intervals and the litter sorted, dried and weighed to establish the seasonality of the culm or leaf fall of each species.

The depth and horizontal extent of the root systems of several individuals of each species were investigated to a depth of one m, at the site of the excavation of several mole-rat burrow systems in the Hutton and Westleigh soils and near a soil pit in the Clovelly soil. The above ground parts and a portion of the root system of an individual of each species was photographed.

ANALYSIS AND PRESENTATION OF DATA

Measurements were usually made during the first week of the month so the difference in shoot or culm length from one month to the next was considered as the shoot or culm elongation during the first month. Only data from "active" shoots or culms, which elongated at some time during the investigation, were included in the calculation of monthly elongation. The data are presented in the form of five-figure summaries or "box and whisker" plots (Underhill, 1981) rather than means and standard deviations which assume a normal distribution of the data. The "box" is delineated by the median, above and below which half the data points fall, and the upper and lower quartiles,

quarter of the data points fall between each of these and the median. The "whiskers" extend from the upper and lower quartiles to the upper and lower extreme values respectively. "Outliers and strays" are represented by single data points.

The L. parile and T. punctatus growth data were statistically tested for significant differences between shoot and culm elongation on the three soils using the non-parametric Mann-Whitney and Kruskall-Wallis tests.

The litter data are incomplete due to the interference of wind, rodents and leaf-eating caterpillars. The presence of leaf or culm material in the litter has been indicated by bar-graphs beneath the shoot or culm elongation data.

RESULTS

Restioid species

Thamnocortus punctatus

During 1980 and 1981 culm development was similar in both sexes on all three soils (Figure 3a, 3b, 3c.) Although there were several differences in the amount of culm elongation there were no significant differences in the seasonality of elongation on the three soils (Table 2, Appendix). New culms emerged from the rhizome during May-June and elongation continued until December-January with a maximum during September to November. After December-January all undamaged culms (save one infertile culm which otherwise developed like the others) produced inflorescences and elongated no further, although they remained green until at least the following June, 11 to 12 months after emerging. Observations of the 1979 and 1980 culms showed that 18 months after emerging, culms exhibited some browning which increased until by January 1982, on the Hutton soil, and March 1982, on both the Clovelly and Westleigh soils, all the 1979 culms were brown and presumably non-photosynthetic, 32 to 34 months after emerging.

The culm component in the litter was small and exhibited no obvious seasonality (Figure 3). Dead culms are not shed immediately but remain attached to the plant as standing-dead material which may constitute as much as 89% of the total dry weight of a 20 year old plant (N.Romoff, pers. comm.).

The root system comprises a densely branched rhizome with shallow, fibrous roots concentrated in the 0 to 10 cm soil layer (Plate 1).

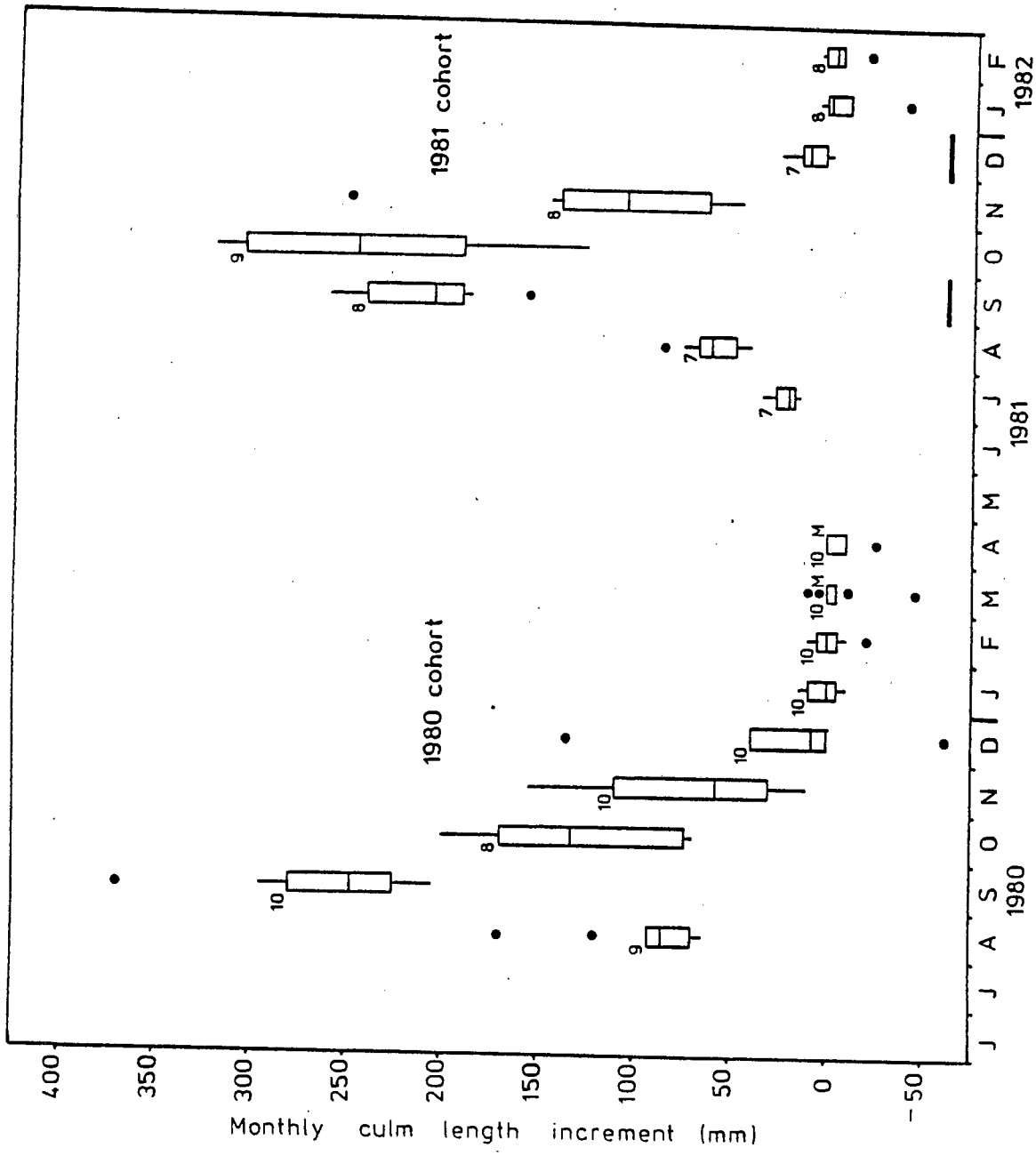


Figure 3a Monthly elongation of labelled T. punctatus culms, on the Hutton soil, August 1980 - April 1981 and July 1981 - February 1982 (box and whisker plots, where the median coincides with either the upper or lower quartile the median is indicated by an m, number of culms indicated above box). Culm litter fall (——).

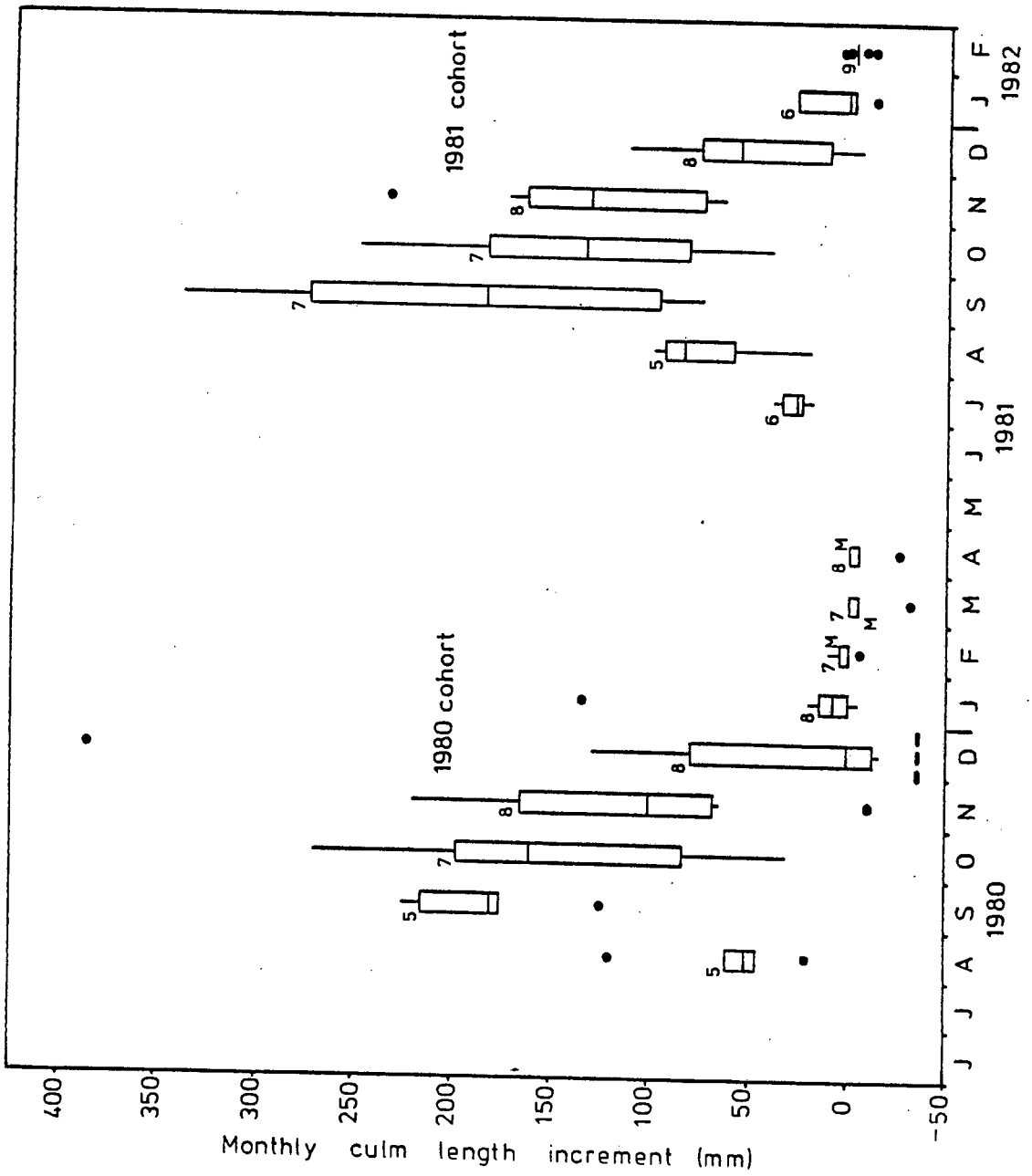


Figure 3b Monthly elongation of labelled T. punctatus culms, on the Clovelly soil, August 1980 - April 1981 and July 1981 - February 1982 (box and whisker plots, where the median coincides with either the upper or lower quartile the median is indicated by an m, number of culms indicated above box). Culm litter fall (— —).

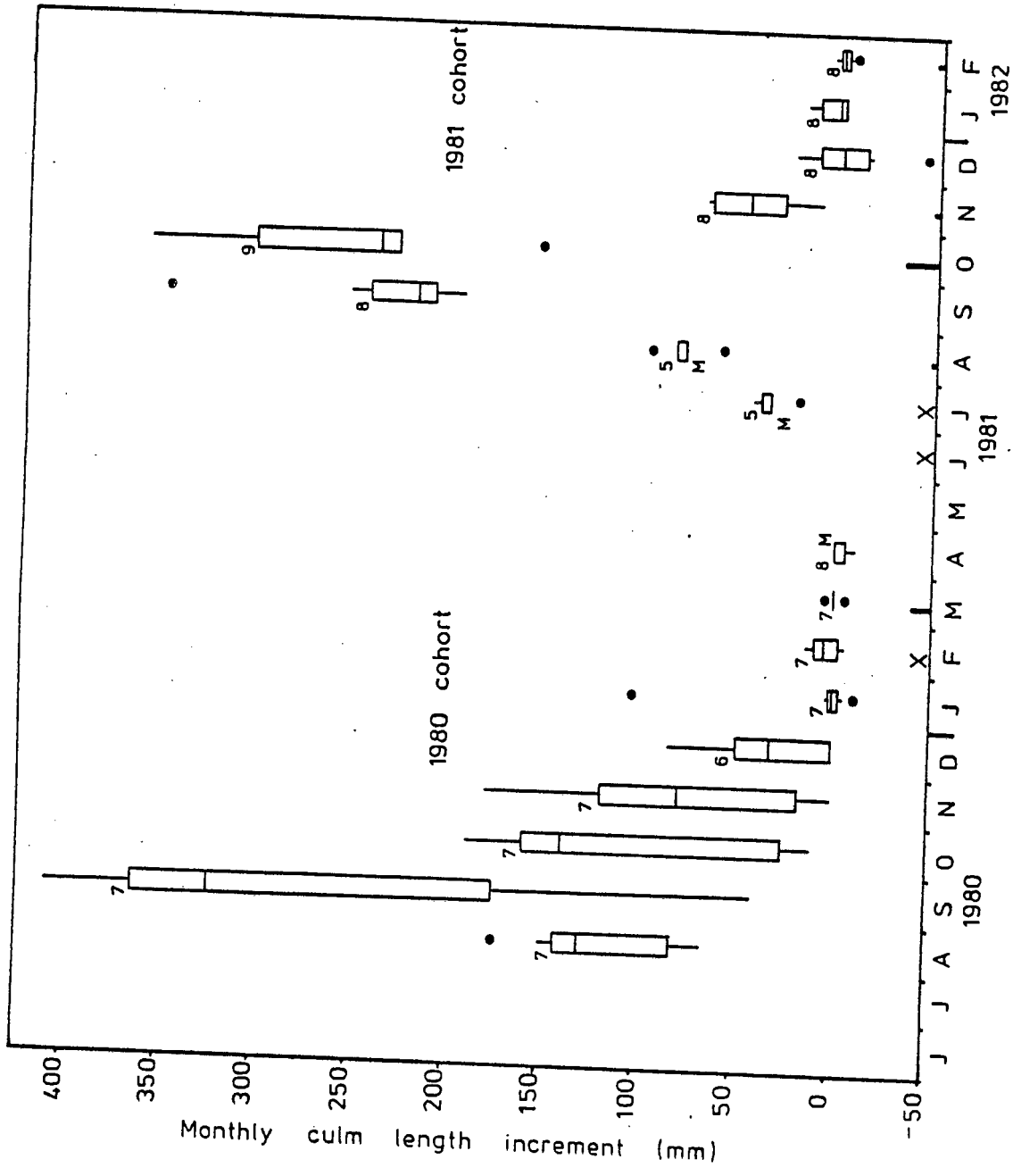


Figure 3c Monthly elongation of labelled T. punctatus culms, on the Westleigh soil, August 1980 - April 1981 and July 1981 - February 1982 (box and whisker plots, where the median coincides with either the upper or lower quartile the median is indicated by an m, number of culms indicated above box). Culm litter fall (I) no sample (X).

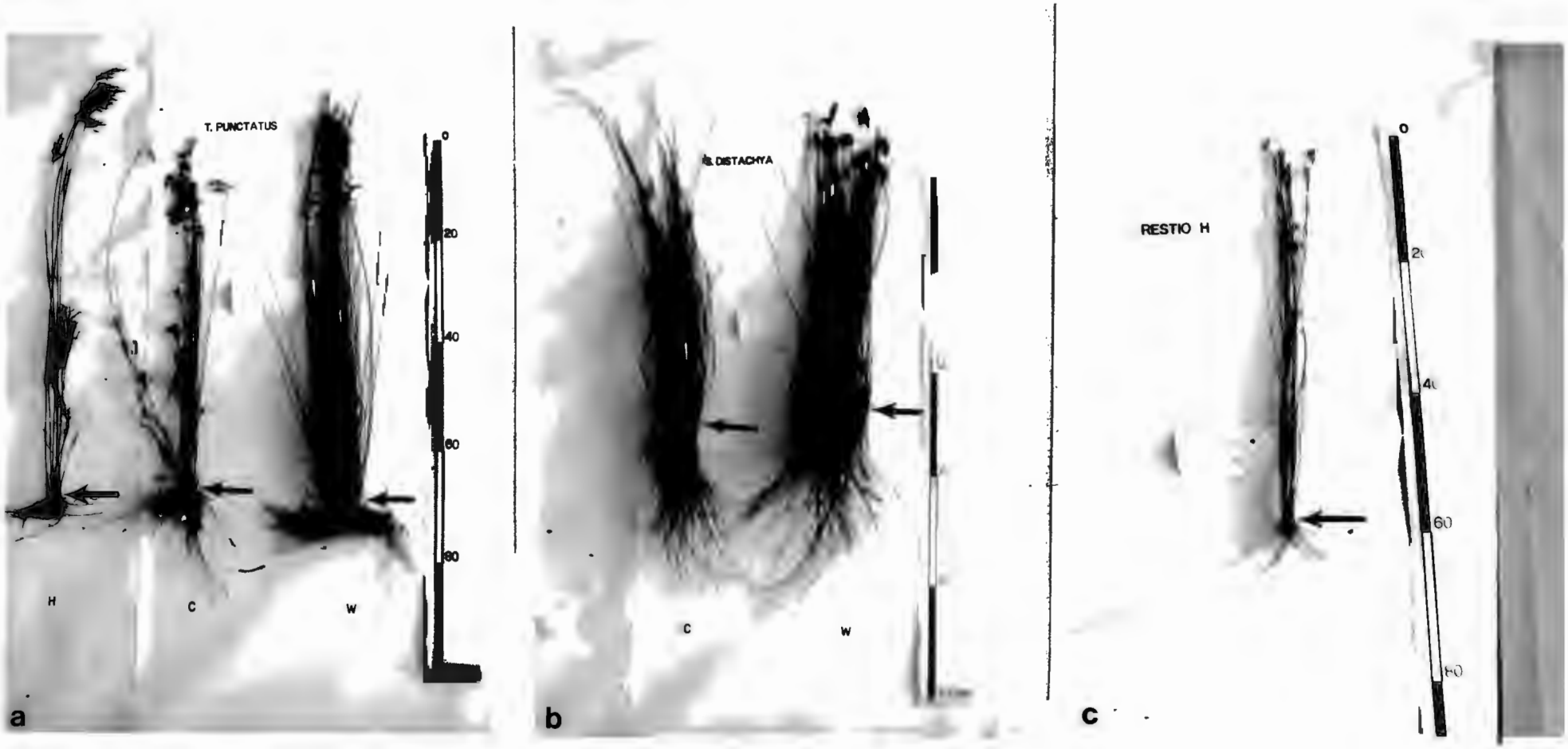


Plate 1 Excavated plants showing root depth of a) T. punctatus on the Hutton H, Clovelly C and Westleigh W soils b) S. distachya on the Clovelly C and Westleigh W soils c) R. monanthus on the Hutton soil. (←) indicates the level of the soil surface

Restio monanthus

Culm elongation occurred almost exclusively from September 1980 to January-February 1981 and was confined to October-November 1981 the following season (Figure 4). Observations of unlabelled culms and plants suggest that this reduction in growth was not as a result of damage to the culms by labelling and measuring. The root system of R. monanthus is superficially very like that of T. punctatus: a densely branched rhizome with shallow fibrous roots (Plate 1).

Staberoha distachya

It is difficult to define a growth period for S. distachya, the data show that there was a relatively high variation in culm elongation throughout the investigation (Figure 5). The Westleigh plants exhibited minimum elongation during January 1981 although considerable elongation occurred during December and February. The general decline from September 1981 is probably related to the fact that no new culms were labelled during this period. The Clovelly data, on the other hand, exhibit an ill-defined peak during December 1980 to April 1981 with minimum median values during November 198(and 1981.

The root system comprises a branched rhizome.with fibrous roots extending to 40 cm (Plate 1).

Proteoid species

Leucospermum parile

During the 1980-'81 growth season there were significant seasonal differences in shoot elongation on the three soils, whereas during 1981-'82 elongation was virtually synchronous (Figure 6, Table 3 Appendix). Shoot elongation occurred from Septemb 1980 to January 1981 on the Hutton soil, from October 1980 to February 1981 on the Westleigh and from November 1980 to March 1981 on the Clovelly. However during 1981-1982 shoot elongation on all three soils began during October and continued unt early March when measurements were terminated.

Comparisons of the elongation of shoots which were measured through both growth seasons show that those on both the Westleigh and Clovelly soils grew equal or smaller amounts during the 1980- '81 season , by comparison with the 1981-'82 season. On the Hutton soil four shoots grew equal amounts, two less and two more during 1980 -'81 by comparison with 1981-'82.

L. parile has a deep tap root system extending to below 1.5m, with the greatest biomass of roots concentrated in the upper 40 cm (S. Jongens-Roberts, pers. comm.). The partial excavations of the root systems of plants in the three soils showed that they were less extensive in the Hutton than in the Clovelly and the Westleigh soils (Plate2

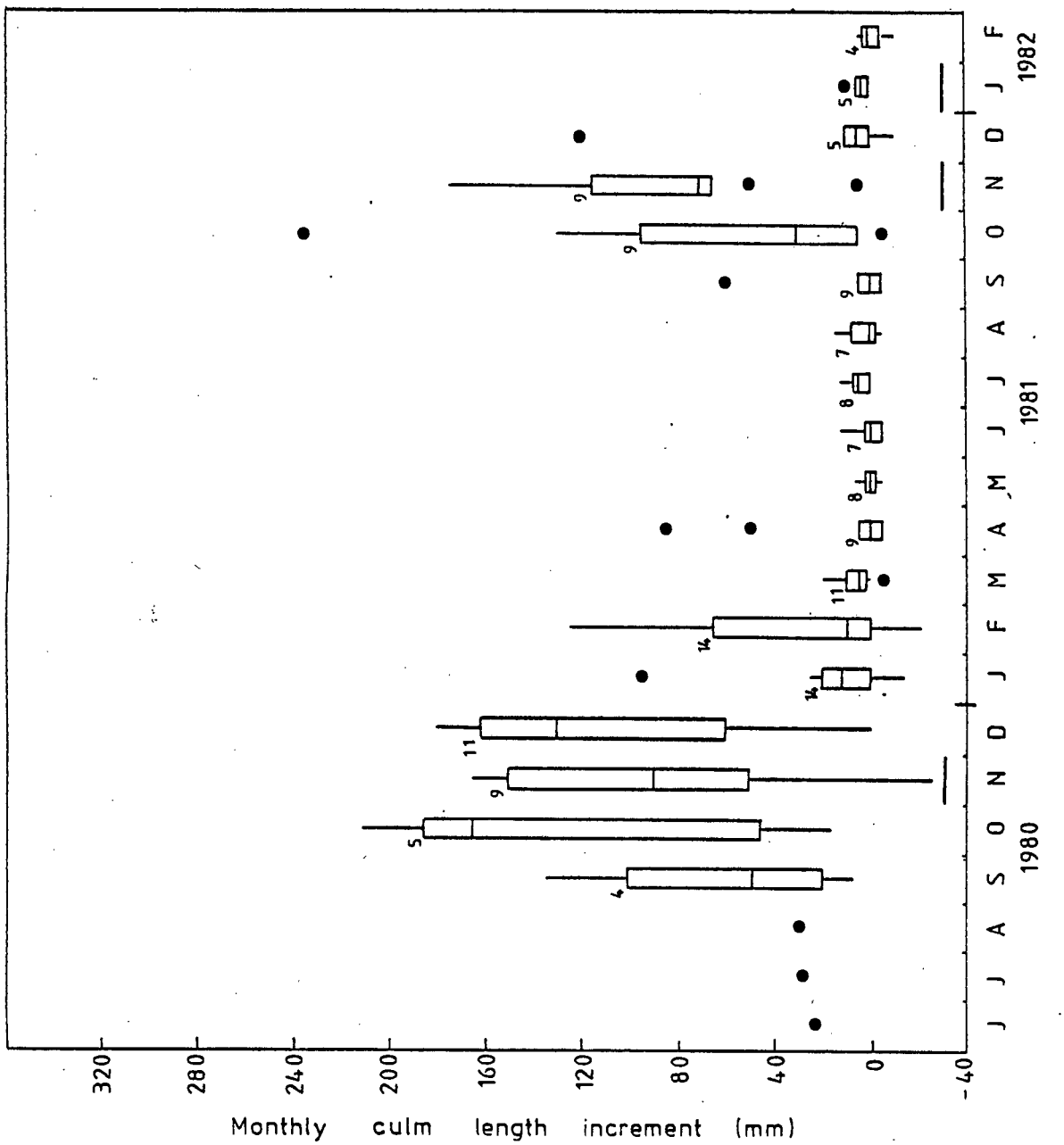


Figure 4 Monthly elongation of labelled R. monanthus culms, on the Hutton soil, June 1980 - February 1982 (box and whisker plots, number of culms indicated above). Culm litter fall (——).

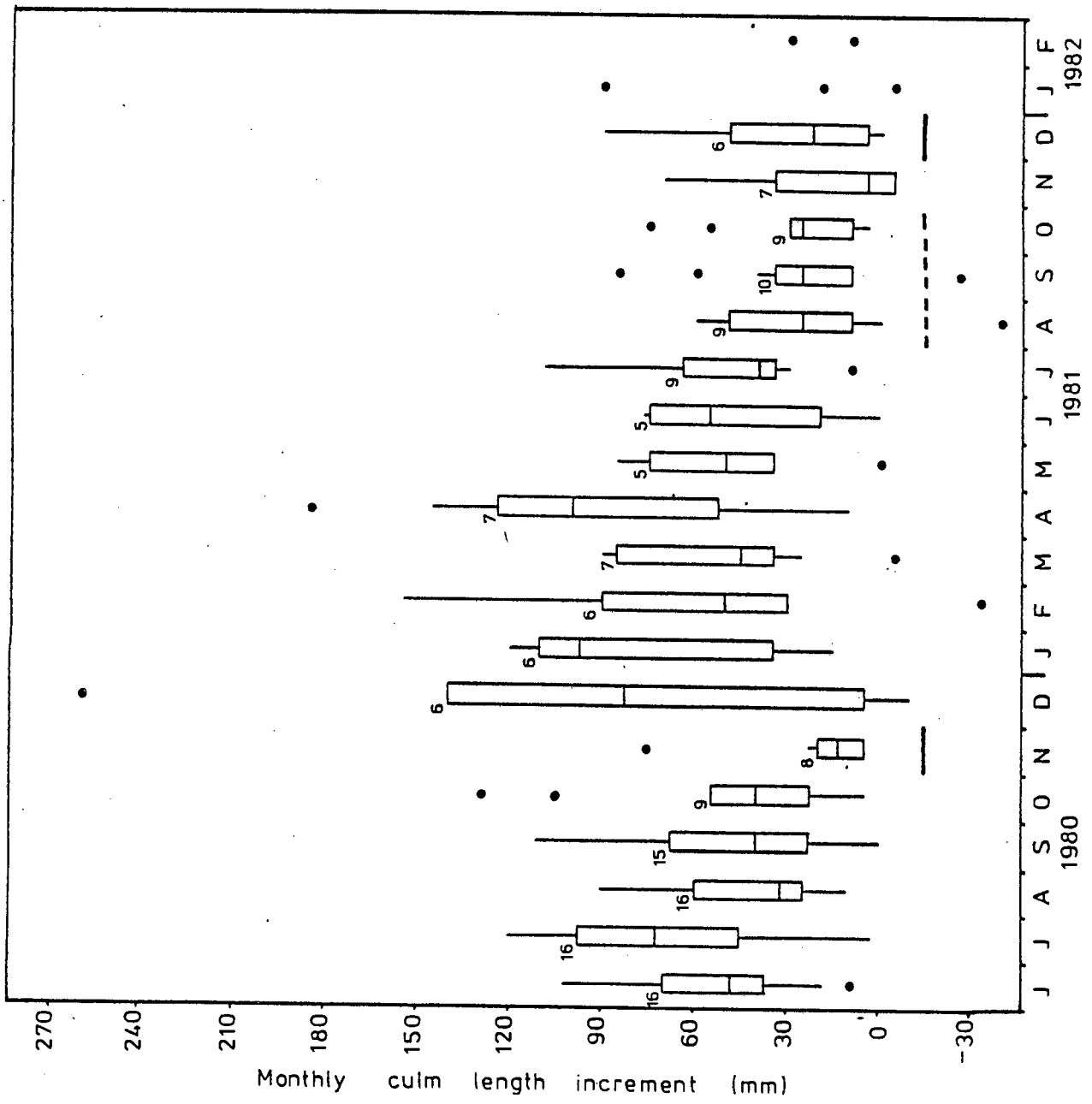


Figure 5a Monthly elongation of labelled S. distachya culms, on the Clovelly soil, June 1980 - February 1982 (box and whisker plots, number of culms indicated above). Culm litter fall (——) maximum, (— —) minimal.

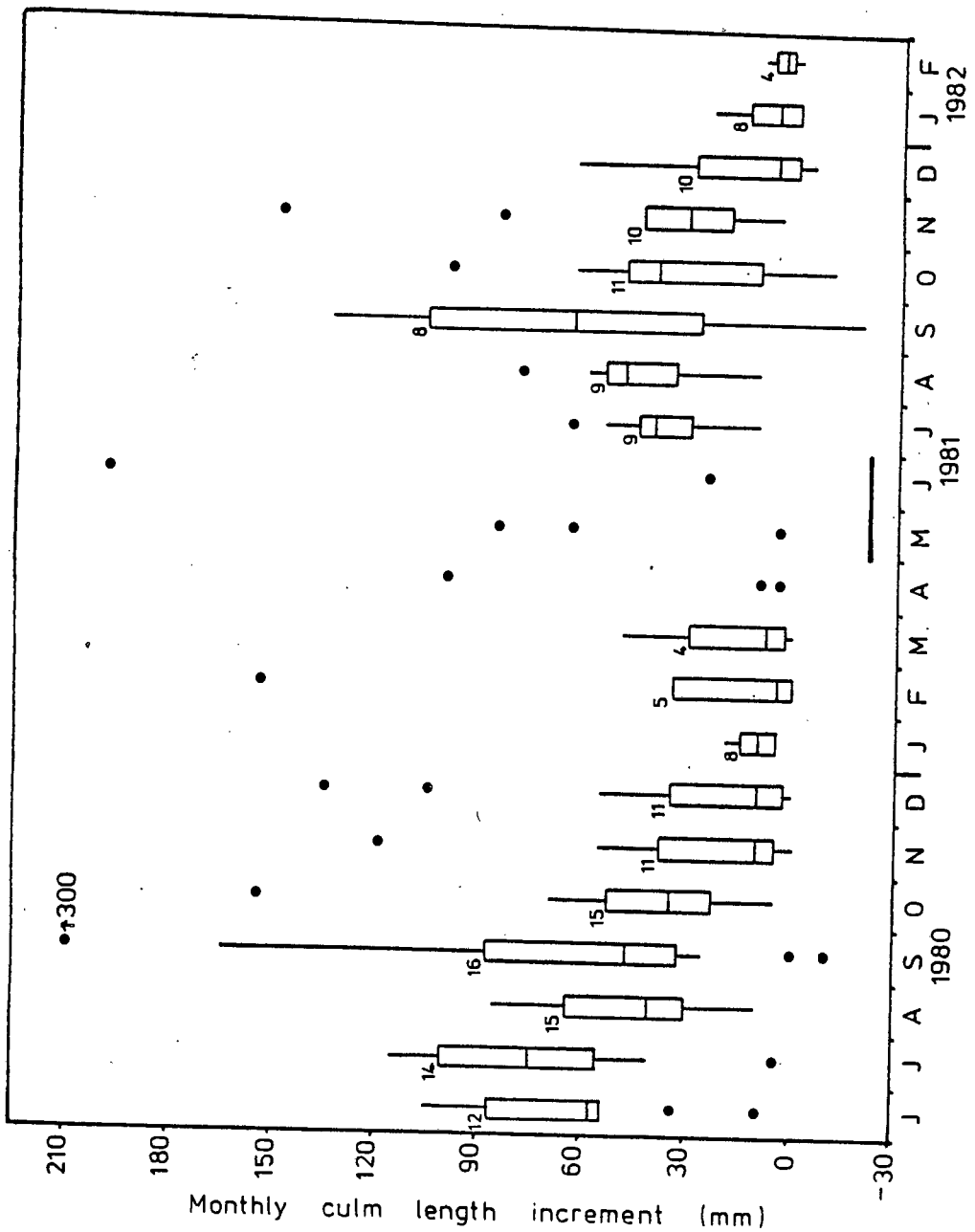


Figure 5b Monthly elongation of labelled S. distachya culms, on the Westleigh soil, June 1980 - February 1982 (box and whisker plots, where the median coincides with either the upper or lower quartile the median is indicated by an m, number of culms indicated above box). Culm litter fall (——).

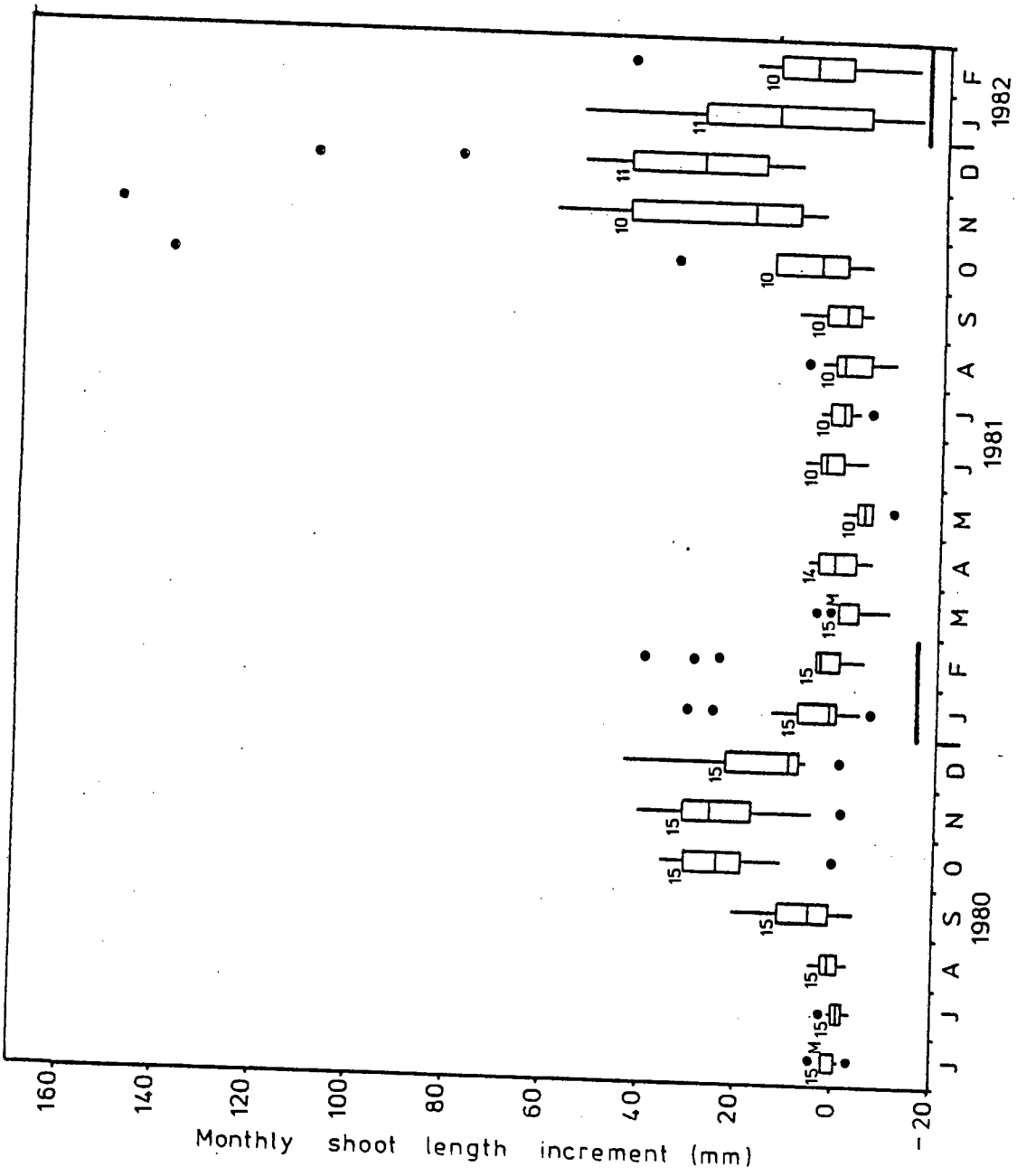


Figure 6a Monthly elongation of labelled L. parile shoots, on the Hutton soil, June 1980 - February 1982 (box and whisker plots, where the median coincides with either the upper or lower quartile the median is indicated by an m, number of culms indicated above box). Leaf fall (——).

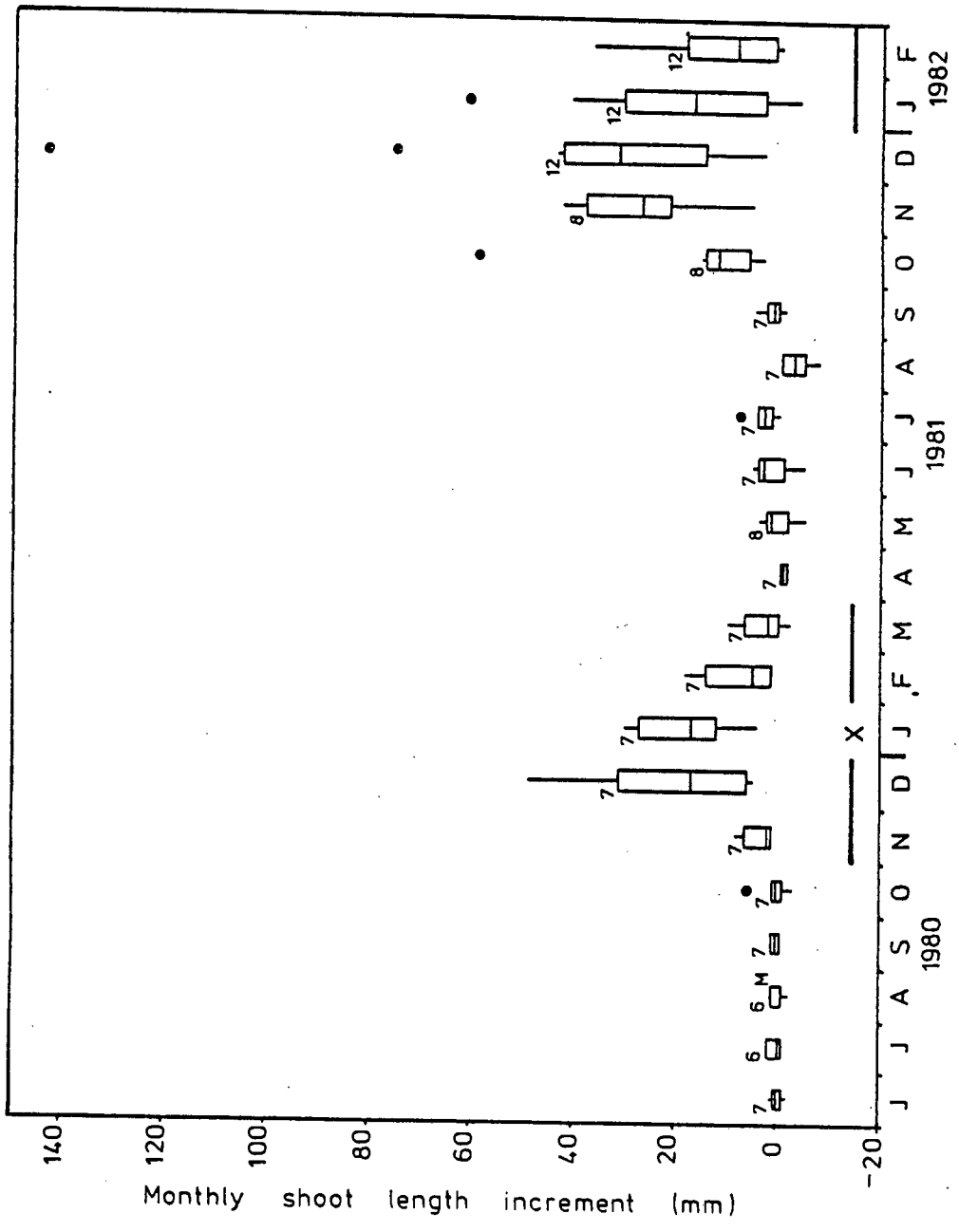


Figure 6b Monthly elongation of labelled L. parile shoots, on the Clovelly soil, June 1980 - February 1982 (box and whisker plots, where the median coincides with either the upper or lower quartile the median is indicated by an m, number of culms indicated above box). Leaf fall (——), no sample (X).

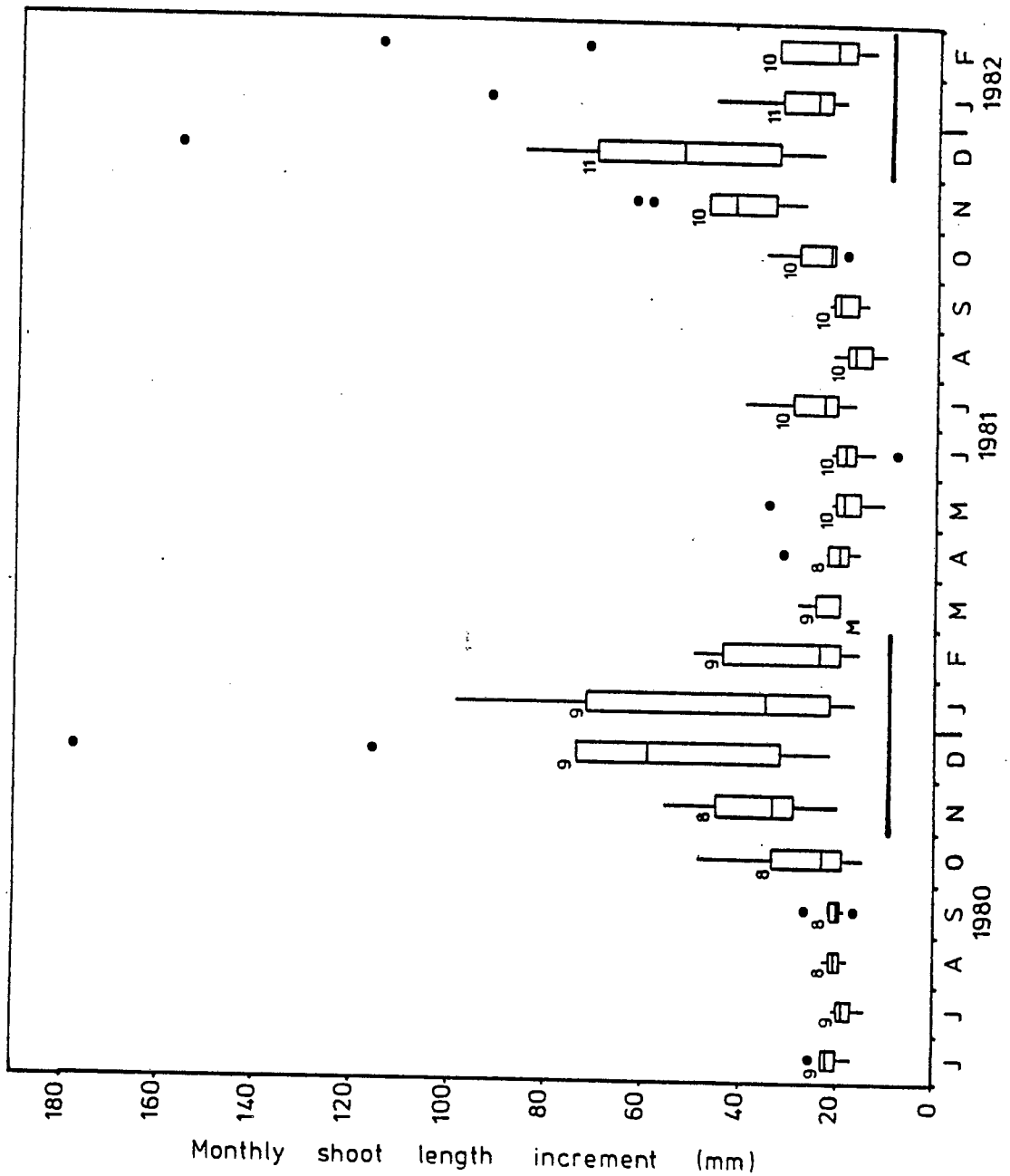


Figure 6c Monthly elongation of labelled L. parile shoots, on the Westleigh soil, June 1980 - February 1982 (box and whisker plots, where the median coincides with either the upper or lower quartile the median is indicated by an m, number of culms indicated above box). Leaf fall (——).

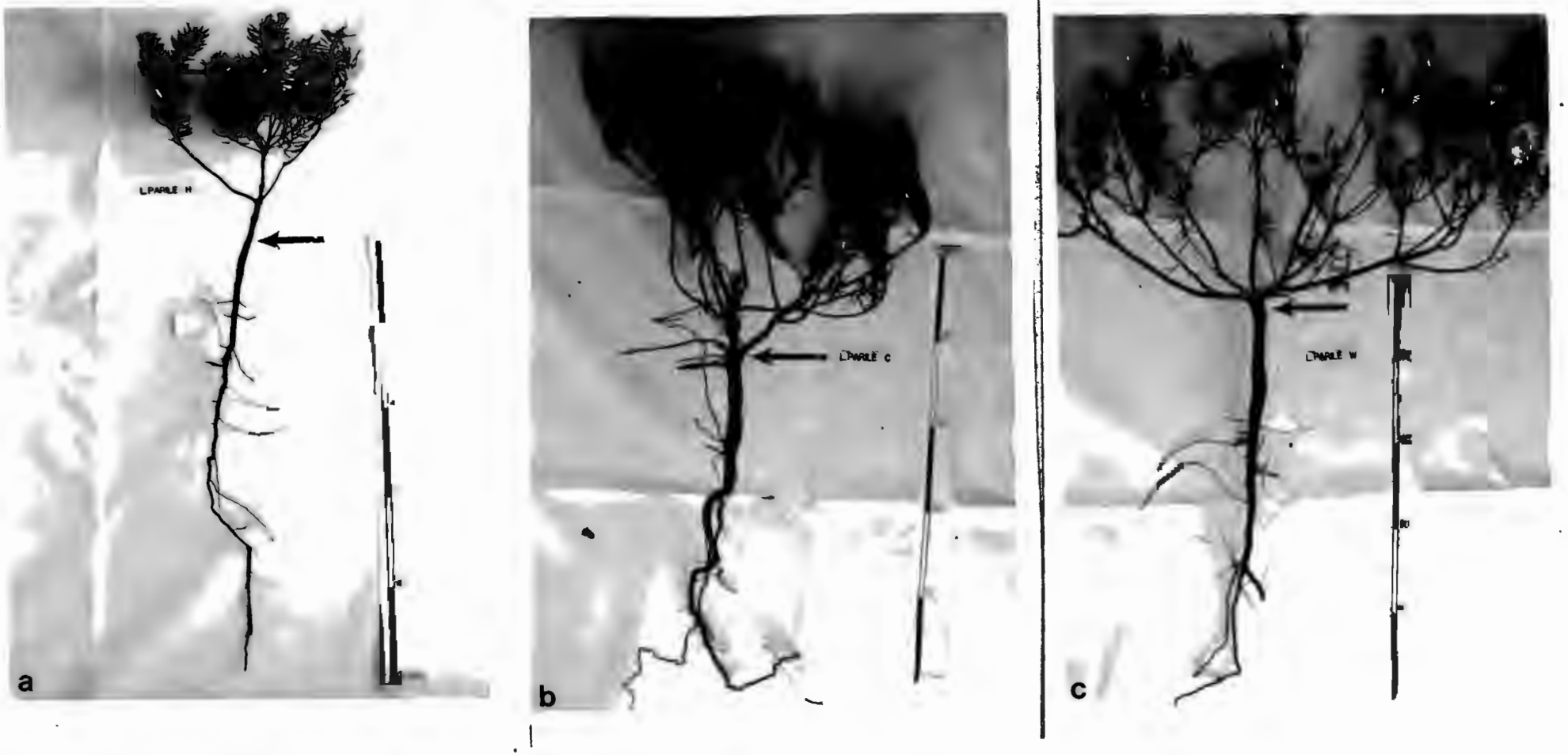


Plate 2 Canopy and portion of the root system of L. parile plant from the a) Hutton H, b) Clovelly C and c) Westleigh W soil. (⟵) illustrates the level of the soil surface

Leucadendron lanigerum

Only six of the 20 labelled shoots elongated during the investigation, during both seasons shoot elongation occurred from December to March (Figure 7). All four shoots which elongated during both seasons grew less during 1980-'81 than during 1981-'82. One of these four shoots was on a male plant, in terms of both season and amount its growth was similar to that of the female shoots.

L. lanigerum resprouts from the rootstock after fire and as a result it had an extensive tap root system (Plate 3).

Diastella proteoides

Shoot growth by elongation and branching occurred predominantly during August to November 1980 and September 1981 to December-January 1982 (Figure 8). However, one shoot grew during September-November 1980, January to March 1981 and October 1981 to February 1982. Of the eight shoots which grew both seasons five grew less during 1980-'81 and three grew comparable amounts.

D. proteoides also resprouts after fire and has an extensive tap root system (Plate 3).

Protea burchellii

Only six of the original ten labelled plants grew in height or by branching during July to September 1980 (Figure 9). Thereafter two dead seedlings were replaced and two shoots labelled on each of the two branched seedlings. During September 1981 to December-January 1982 11 of the 12 labelled shoots or plants grew. The tap root system of the P. burchellii seedlings was not extensive although a slender tap root extended to below 1 m (Plate 3).

Ericoid species

Metalasia muricata

The timing of shoot growth, by elongation and branching, on both the Clovelly and Westleigh soils was similar but the shoots on the Westleigh soil grew more both seasons (Figure 10). The shoots which were measured throughout grew less during 1980-'81 than during 1981-'82, bar one for which the reverse was true.

The root system of M. muricata in both soils was a shallow tap root system concentrated in the upper 20 cm (Plate 4).

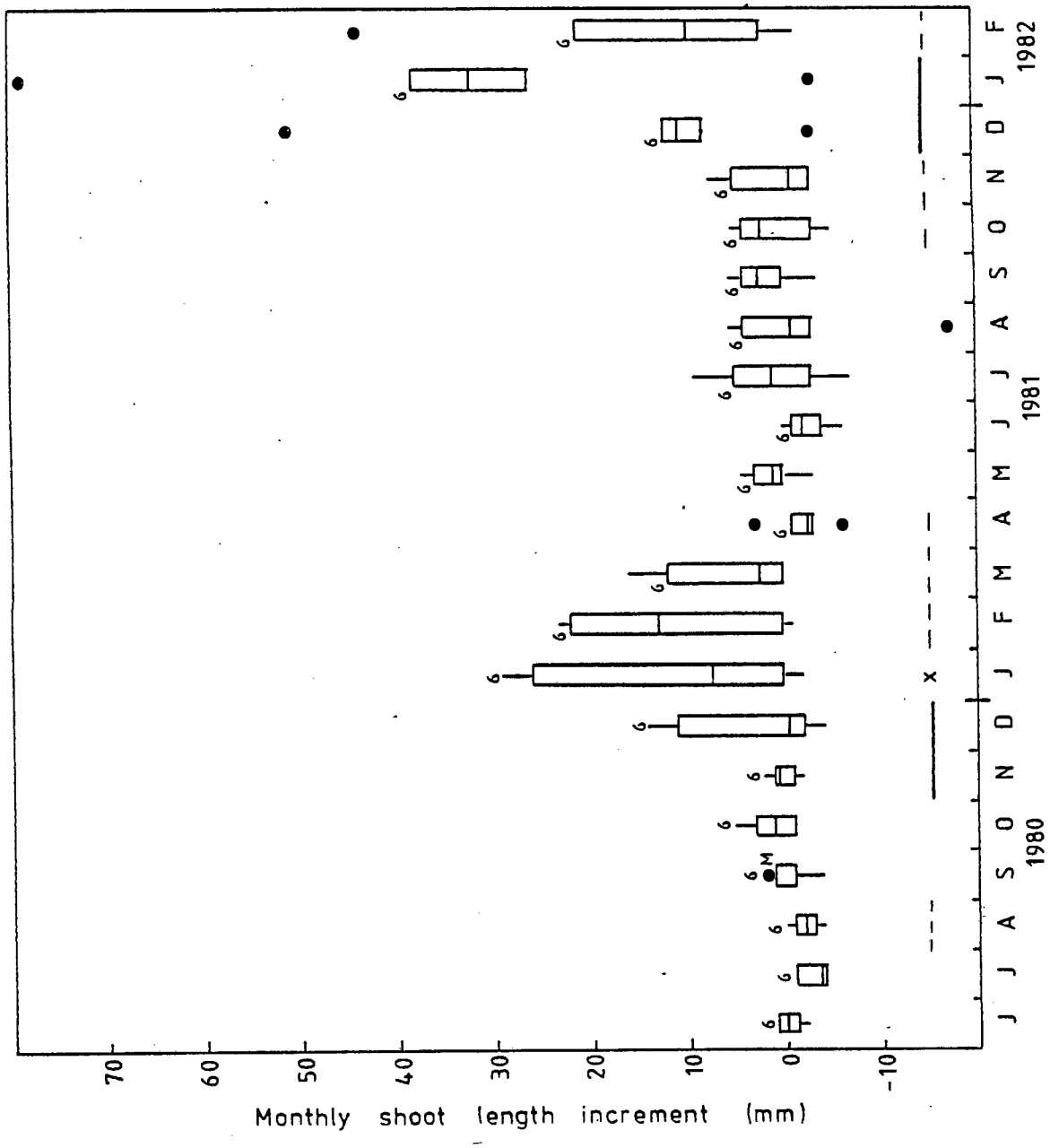


Figure 7 Monthly elongation of labelled L. lanigerum shoots, on the Hutton soil, June 1980 - February 1982 (box and whisker plots, where the median coincides with either the upper or lower quartile the median is indicated by an m, number of shoots indicated above). Maximum leaf fall (——), minimal (— —), no sample (X).

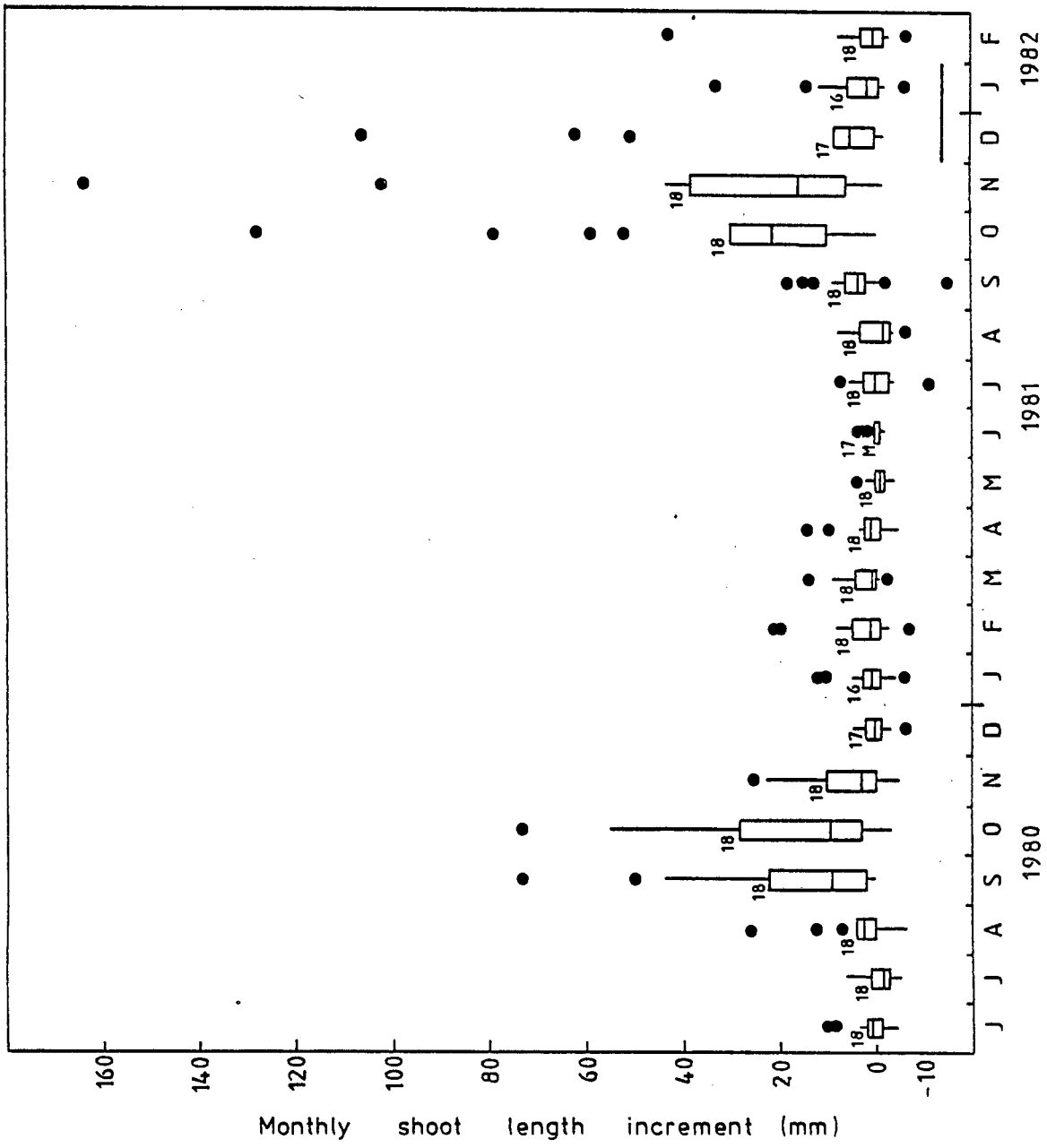


Figure 8 Monthly elongation of labelled D. proteoides shoots, on the Westleigh soil June 1980 - February 1982 (box and whisker plots, where the median coincides with either the upper or lower quartile the median is indicated by an m, number of shoots indicated above). Maximum leaf fall (——).

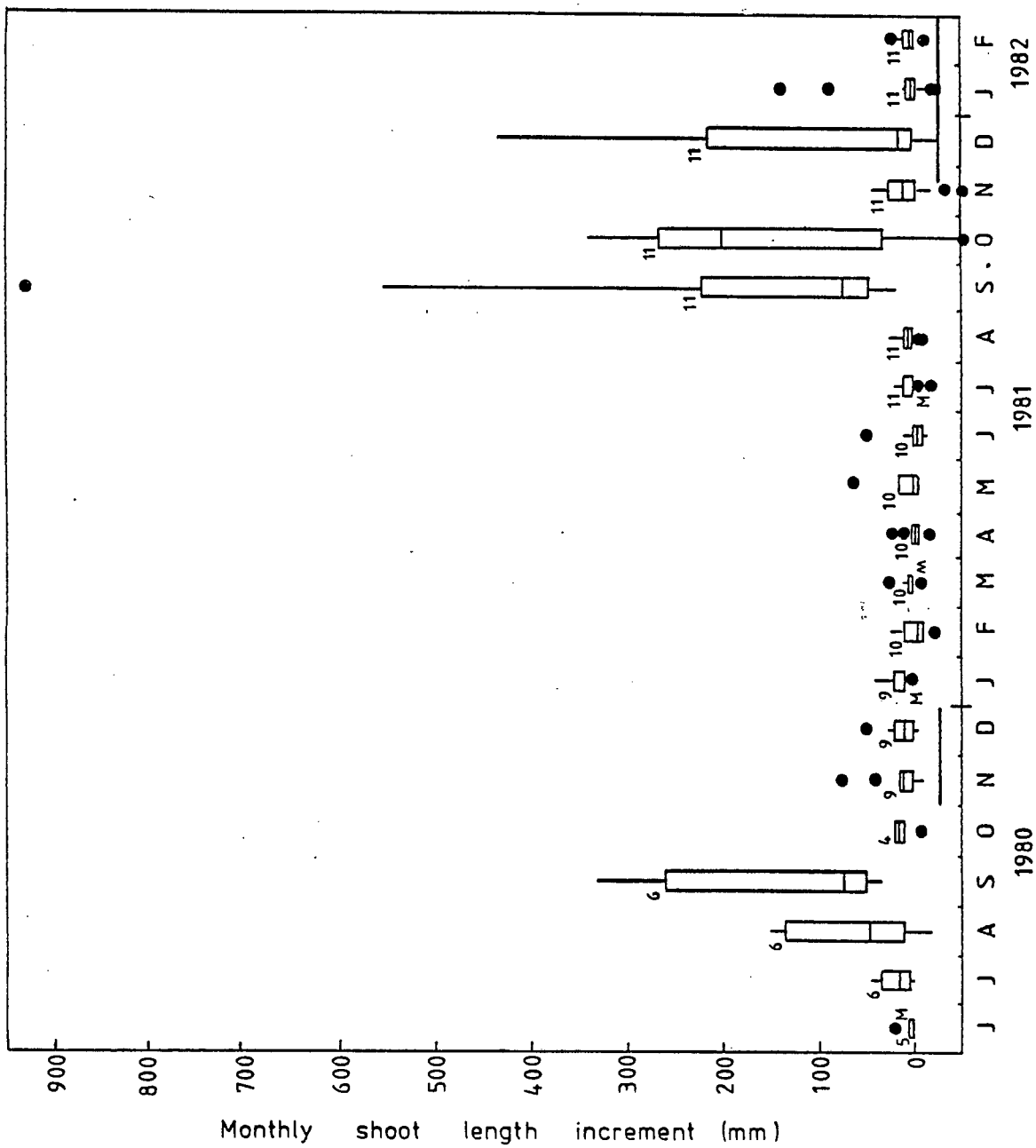


Figure 9 Monthly elongation of labelled P. burchellii shoots, on the Hutton soil, June 1980 - February 1982 (box and whisker plots, where the median coincides with either the upper or lower quartile the median is indicated by an m, number of shoots indicated above). Maximum leaf fall (——).

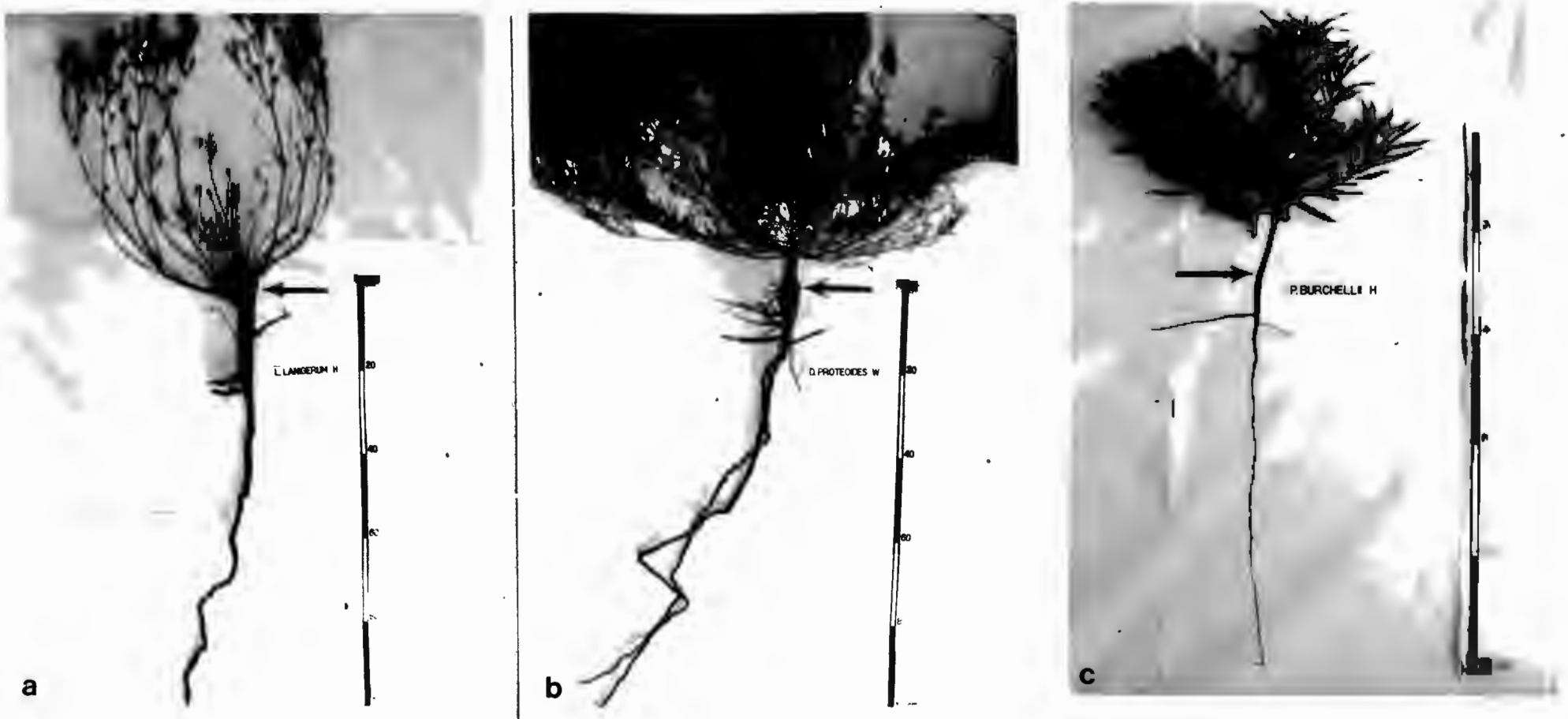


Plate 3 Canopy and portion of the root system of a) L. lanigerum on the Hutton soil, b) D. proteoides on the Westleigh soil and c) P. burchellii on the Hutton soil. (←) indicates the level of the soil surface

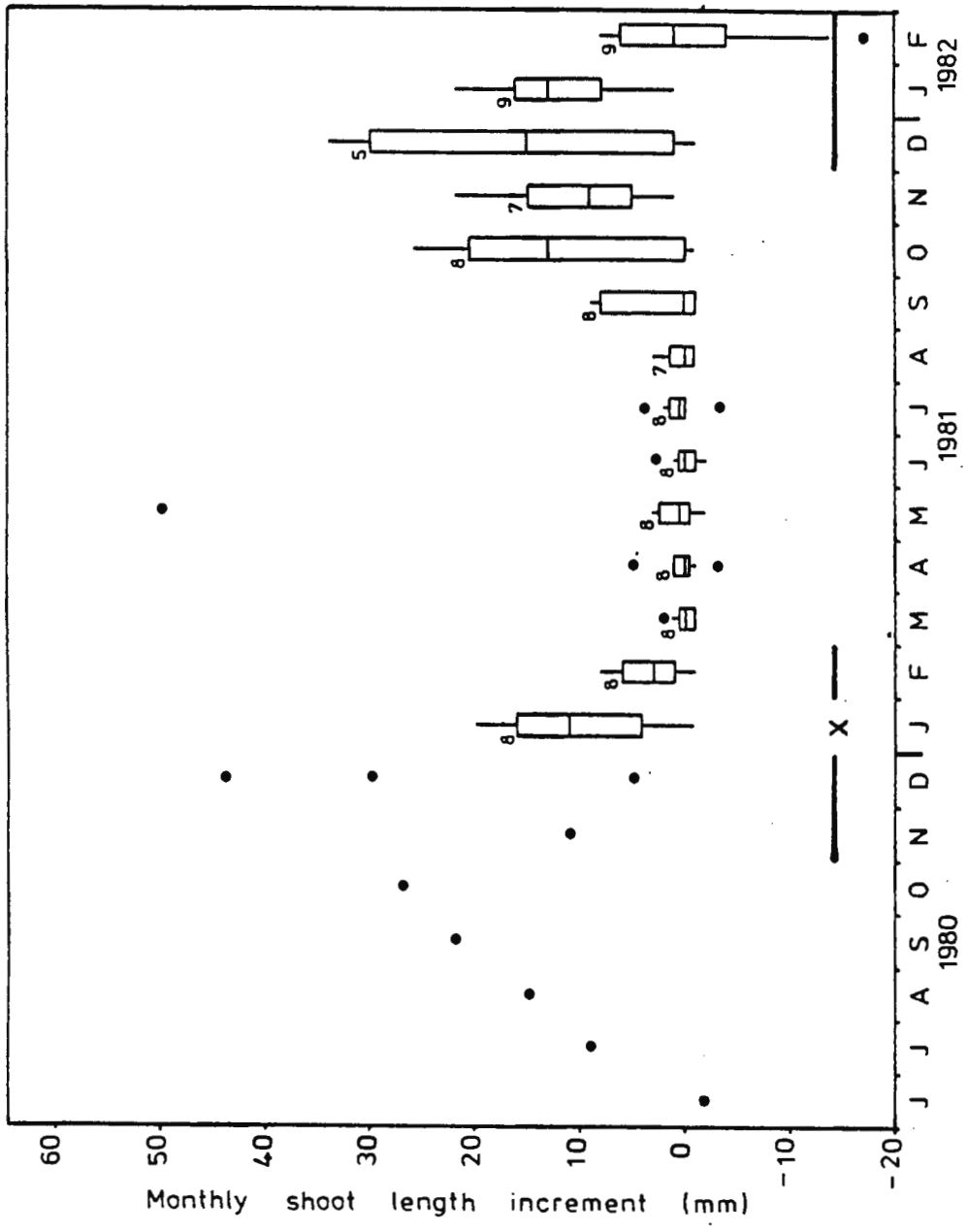


Figure 10a Monthly elongation of labelled M. muricata shoots, on the Clovelly soil, June 1980 - February 1982 (box and whisker plots, number of shoots indicated above). Leaf fall (——), no sample (X).

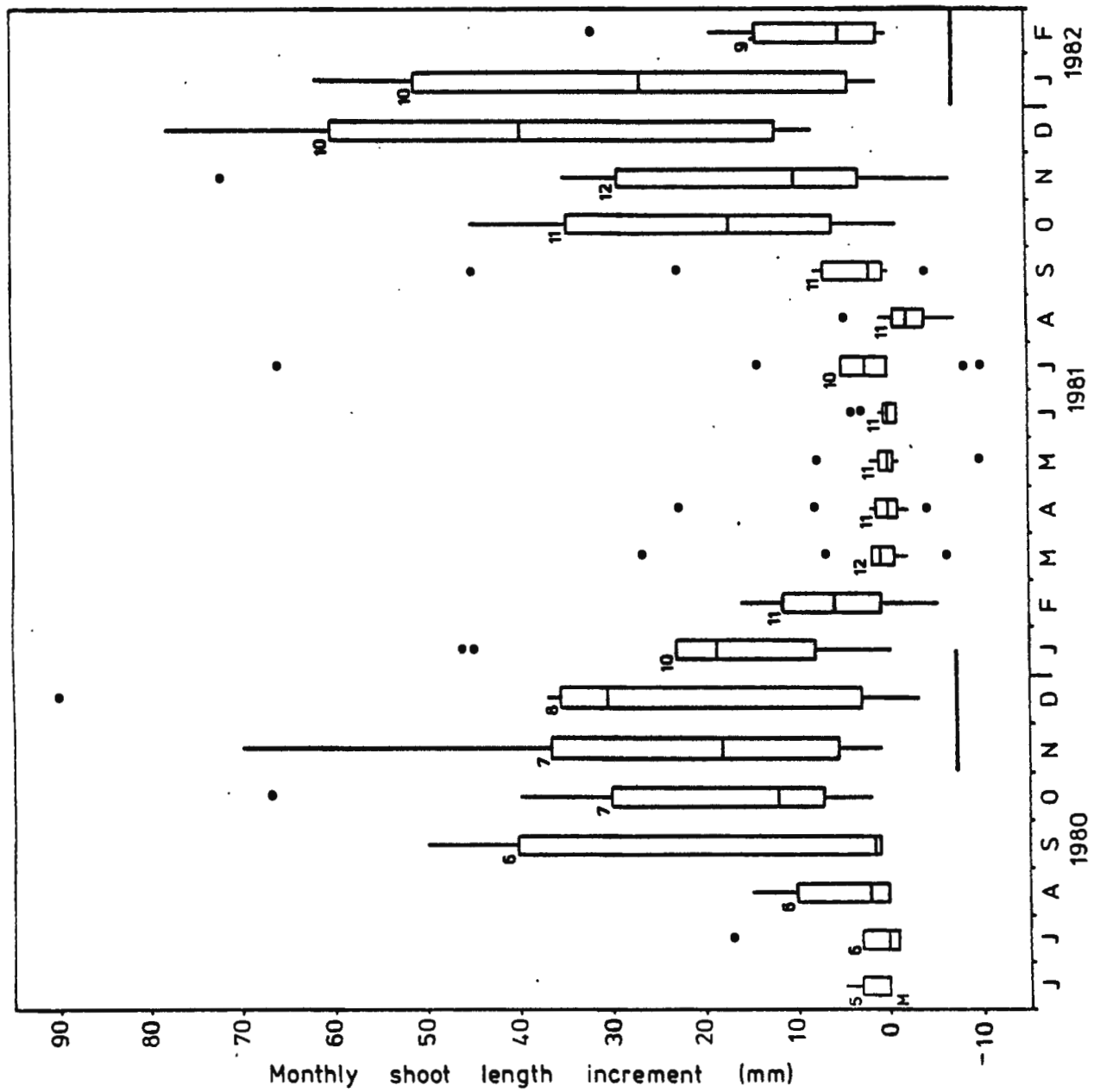


Figure 10b Monthly elongation of labelled M. muricata shoots, on the Westleigh soil, June 1980 - February 1982 (box and whisker plots, where the median coincides with either the upper or lower quartile the median is indicated by an m, number of shoots indicated above). Maximum leaf fall (——)

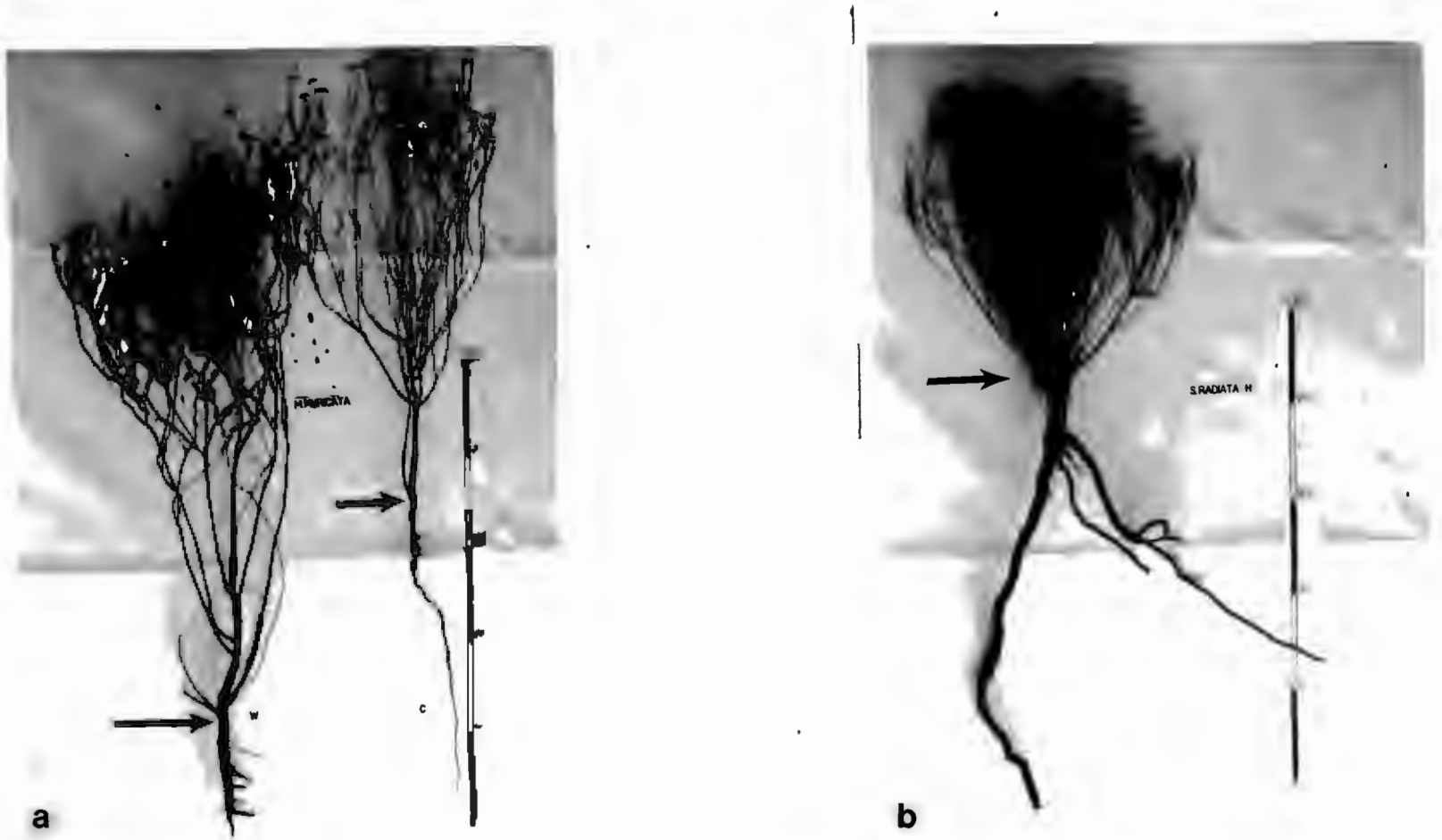


Plate 4 Canopy and portion of the root system of a) M. muricata on the Clovelly C and Westleigh W soil and b) S. radiata on the Hutton soil. (⟶) indicates the soil surface

Staavia radiata

Shoot growth occurred predominantly during October-November to February-March both seasons (Figure 11). All four of the shoots which were measured throughout grew comparable amounts during both growth seasons.

S. radiata resprouts after fire and has an extensive tap root system (Plate 4).

Berzelia abrotanoides

Shoot growth by elongation occurred virtually throughout the investigation with a minimum during March-April 1981 and maxima between September and December of both 1980 and 1981 (Figure 12). Those shoots which were measured throughout grew very little if at all after February 1981; this may be related to shoot damage by labelling and measuring.

B. abrotanoides resprouts after fire but unlike the other shrub species it has several large primary roots which spread horizontally and appear to be largely confined to the upper 60 cm of the soil (Plate 5).

Grisebachia plumosa

During 1980-'81 shoot growth occurred in an ill-defined period from July 1980 to April-May 1981 (Figure 13). Of the 16 shoots measured throughout none exhibited shoot growth after May 1981, although this may be attributed to shoot damage, observations of unlabelled plants indicated that little shoot growth occurred during this period.

The quality of leaf litter collected during October to December 1981 was considerably higher than that collected during the previous year.

G. plumosa has a shallow, non-extensive tap root system largely confined to the upper 30 cm (Plate 5).

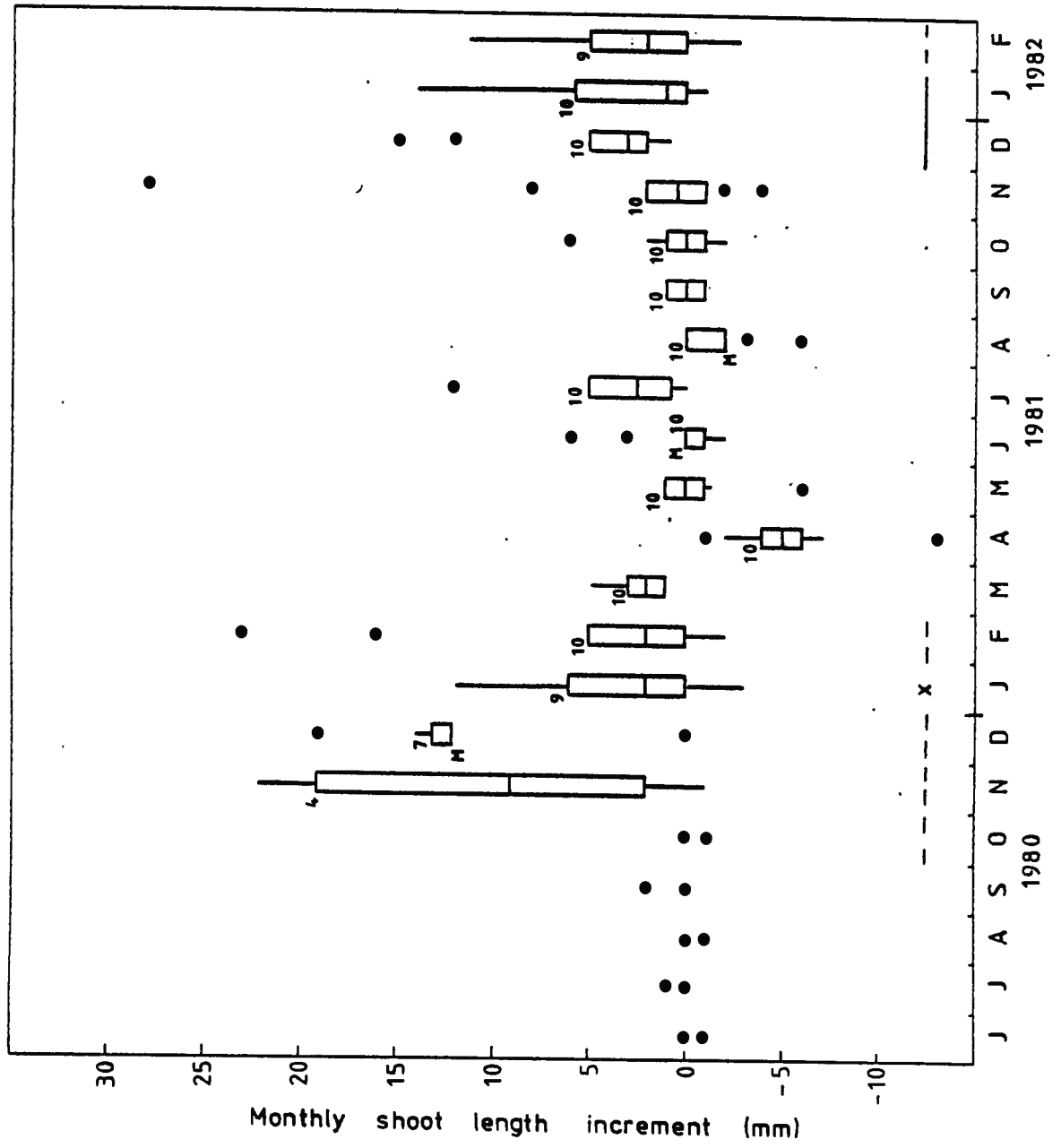


Figure 11 Monthly elongation of labelled S. radiata shoots, on the Hutton soil, June 1980 - February 1982 (box and whisker plots, where the median coincides with either the upper or lower quartile the median is indicated by an m, number of shoots indicated above). Maximum leaf fall (——) minimal (— —), no sample (X).

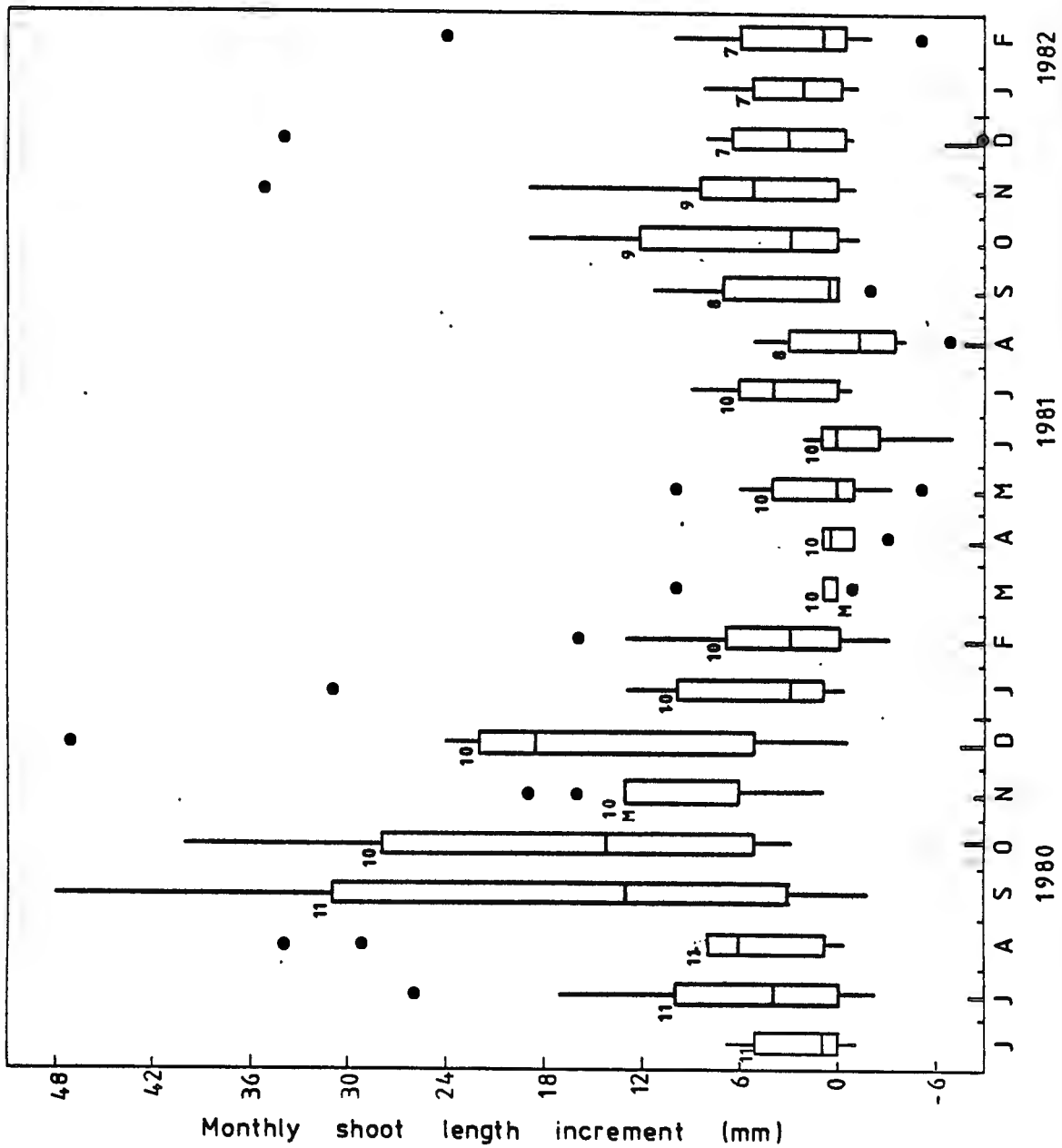


Figure 12 Monthly elongation of labelled B. abrotanoides shoots, on the Westleigh soi June 1980 - February 1982 (box and whisker plots, where the median coincides with either the upper or lower quartile the median is indicated by an m, number of shoots indicated above). Leaf litter (I).

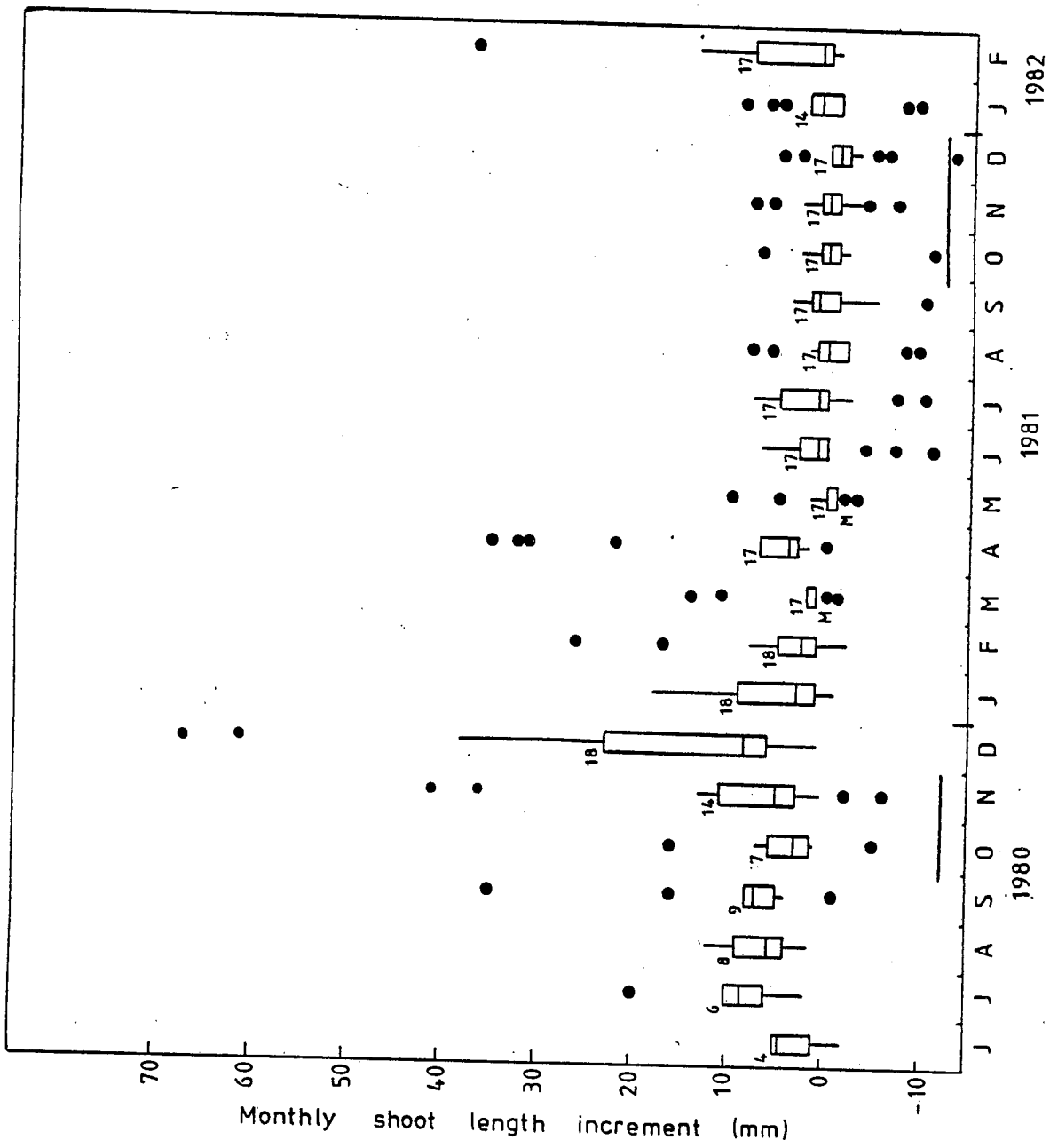
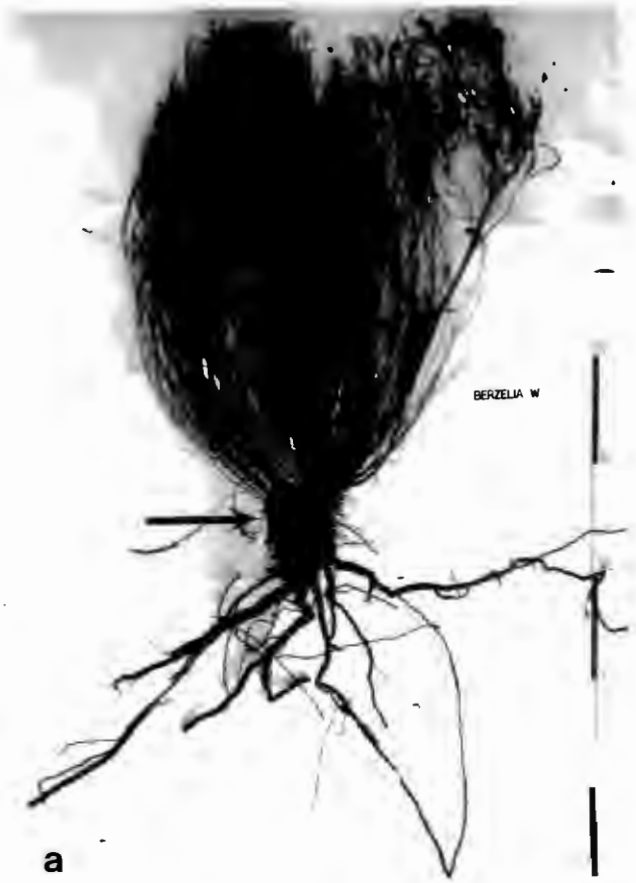


Figure 13 Monthly elongation of labelled G. plumosa shoots, on the Clovelly soil, June 1980 - February 1982 (box and whisker plots, where the median coincides with either the upper or lower quartile the median is indicated by an m, number of shoots indicated above). Maximum leaf fall (——).



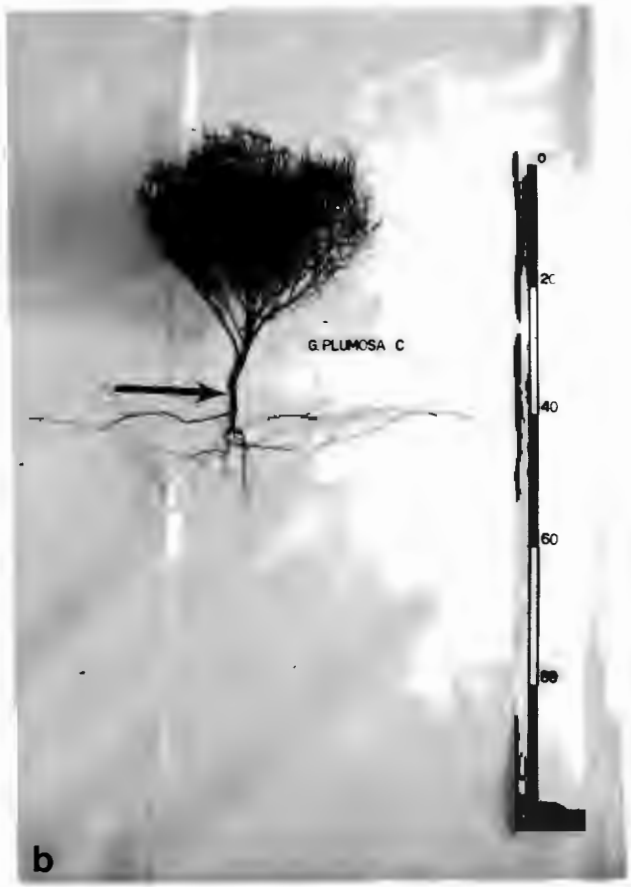


Plate 5 Canopy and portion of the root system of a) B. abrotanoides on the Westleigh soil and b) G. plumosa on the Clovelly soil. (⟶) indicates the soil surface

DISCUSSION

Most of the species investigated grew at some time during spring and summer. Only *L. lanigerum* grew during summer and early autumn and *B. abrotanoides* and *S. distachya* grew virtually throughout the investigation. There is no obvious correlation between these three, or any other growth form groups, and the season of shoot or culm growth. This contrasts with Bond's (1980) observation that "growth seasons within similar life forms were strikingly similar" in southern Cape mountain fynbos. On the basis of data predominantly from south western Cape mountain fynbos Kruger (1981) suggests that although there is a "broad correlation between phenology and growth or life form ... this is not necessarily consistent". A synthesis of available fynbos seasonal growth data led Pierce (in prep.) to conclude that "Generalisations regarding seasonality in growth forms are not possible and neither are classifications of species into groups with similar seasonal patterns".

There appears to be some relationship between the timing of shoot or culm growth and factors such as root depth and/or extent, plant water-use efficiency, soil-moisture-holding capacity and plant age.

Several workers in other mediterranean-type communities have related the growth of some species late in the dry spring-summer to the ability of their deep roots to utilise soil moisture not available to other shallower rooted species (Mooney and Dunn 1970, Aljaro et al. 1972, Pierce and Cowling in prep.) *T. punctatus* commenced culm growth earlier than other species investigated; this may be related to its shallow root system, confined to the upper soil layer which dries out earlier than deeper layers (Brown et al. in press, Sommerville and Moll in prep.). In addition the absorptive root cortex layer is shed under conditions of moisture stress (J. Hardcastle pers. comm.). Measurements of culm xylem pressure potential confirm that *T. punctatus* experiences increasing moisture stress during spring-summer with a dramatic rise in February, synchronous with the termination of culm growth.

The growth of *R. monanthus* during February 1981 suggests that this species was not as moisture stressed as *T. punctatus*, in spite of having a superficially similar root system. This was confirmed by an isolated measurement of xylem pressure potential on *R. monanthus* in February 1982 (Sommerville and Moll, unpubl. data). *S. distachya* has deeper roots than *T. punctatus* and *R. monanthus* and as such should be less

affected by spring-summer decreases in soil moisture. This was confirmed by the culm growth observed throughout the investigation and by an isolated measurement of xylem pressure potential in February 1982 (Sommerville and Moll, unpubl. data).

The earlier commencement of shoot growth in L. parile, by comparison with that of L. lanigerum which resprouts from the rootstock after fire and therefore had a more extensive root system, provides further evidence of the relationship between root extent and growth season. However the observed growth of G. plumosa and M. muricata during spring-summer, similar to L. parile which has a more extensive root system, suggests that growth season and root extent are not necessarily directly related.

The growth of G. plumosa and M. muricata relative to L. parile and of R. monanthus by comparison with T. punctatus may be related to differences in the efficiency of their water usage. G. plumosa, M. muricata and R. monanthus may lose less water by transpiration and have a lower water requirement for growth than L. parile and T. punctatus. Similarly the predominantly spring growth observed in D. proteoides by comparison with the summer growth in L. lanigerum may be related to its smaller, apparently less sclerophyllous leaves (pers. obs.) which may lose water faster than those of L. lanigerum. However, other factors such as differences in photoperiod and temperature requirements may be involved.

The observed differences in the growth season of L. parile on the three soils during 1980-'81 may be attributed to their different water-holding capacities. The Hutton soil has a higher water-holding capacity than the Clovelly soil (M. Fry, pers. comm.) and as a result plant-available moisture may become limiting earlier in the Hutton soil. Water probably drains through the coarser Westleigh soil faster than through the Clovelly soil, with similar effect. Unfortunately during 1981-'82, when plant and soil moisture were measured (Somerville and Moll, in prep.), growth was almost synchronous on all three soils. The difference in shoot growth between years may be explained by differences in rainfall, there being less winter rain during the winter months before growth in 1980 than in 1981 (Figure 1). Since the timing of the commencement of growth varied it seems likely that some minimum level of plant-available moisture may be involved in the initiation of shoot growth in L. parile (cf Kummerow et al., 1981). The smaller size of the canopies of L. parile plants on the Hutton soil (Table 4, Appendix) may be further evidence of the lower moisture-availability in these soils. It has been suggested that a non-sprouting chaparral species survives drought by the sacrifice of

certain branches "with the surviving ones preferentially receiving available resources" (Parsons et al., 1981). Plants on the Hutton soil may be small as a result of a reduction in the number of shoots produced during dry years such as 1980-'81, when moisture-stress was higher in this soil.

Differences in the amount and timing of shoot or culm growth in P. burchellii, R. monanthus and G. plumosa during 1980-'81 and 1981-'82 suggest that the age of a plant affects its growth season. P. burchellii grew more, over a longer period and commencing later during 1981-'82 than 1980-'81. I attribute this to both the heavier winter rains (Figure 1) and the growth of the root system. Unfortunately the 20 year old labelled plants were burnt in an accidental fire so there are no data to show whether growth season becomes even later as the root system grows even more extensive. There was a considerable reduction in the culm and shoot growth of R. monanthus and G. plumosa, respectively, during 1981-'82 by comparison with 1980-'81. This contrasts with the other species investigated which grew similar or greater amounts during 1981-'82 by comparison with 1980-'81. I suggest that R. monanthus and G. plumosa are relatively short-lived species which were beginning to senesce during 1981-'82. This is supported by the fact that both these species were most common in four year old communities and by their low occurrence in older communities at Pella (Boucher and Shepherd, in prep.).

Comparisons with other fynbos data

There are several interesting comparisons between these data and the results of other investigations of fynbos species phenology. There are no other reports of restioid species growing throughout the year as S. distachya did, suggesting that its relatively deep roots may be unusual in this group. It has been reported that there is a trend of earlier growth, in restioid species, eastwards across the fynbos biome (Pierce and Cowling, in prep.). The maximum growth periods of T. punctatus and R. monanthus fall within the spring-summer period described for south western Cape species (Kruger 1981, Pierce in prep.). This is earlier than the autumn-spring period for south eastern Cape species (Pierce and Cowling, in prep.) and the winter-spring period for southern Cape species (Bond, 1980). However, this distinction is not clear since T. punctatus commenced growth during winter and some summer growth was recorded in both the south eastern and southern Cape.

The observed growth of L. parile during spring-summer contrasts with the summer-autumn period reported for other Leucospermum species in the south western and south eastern Cape (Kruger 1981, Pierce and Cowling in prep.) The spring-summer growth of P. burchellii agrees with Kruger's (1981) observations of other south western Cape Protea species, but may extend beyond this period in older plants. The L. lanigerum growth season is similar to that of other fynbos Leucadendron species (Williams 1972, Bond 1980, Kruger 1981, Pierce and Cowling in prep.) Pierce (in prep.) attributes the varied growth seasons observed in small-leaved sclerophyll shrubs (equivalent to my ericoid group) to the taxonomic and growth form heterogeneity of this group. But in this investigation the variation observed in growth seasons within the more homogeneous proteoid and restioid groups was comparable with that within the ericoid group.

Discussion with reference to current thinking

There does not appear to be consensus as regards the temperate or tropical origins of the Proteaceae (Beard 1959, Burbidge 1960, Axelrod and Raven 1978, cf Levyns 1958, Johnson and Briggs 1963, Raven and Axelrod 1974, Goldblatt 1978). This is perhaps mirrored by the observed variation in the growth seasons of these four species, ranging from late winter-spring to summer-early autumn. But the growth of sub-tropical species like Pterocelastrus tricuspidatus and Sideroxylon inerme during the cooler months in the south eastern Cape conflicts directly with the "past climate" theory (Pierce, in prep.). An investigation of the different temperature responses of growth in several Australian Banksia species suggests that the growth responses of these species may be related to present rather than past climate as Specht and Rayson (1957) suggested (Groves, 1978).

In terms of present climate there are no obvious correlations between growth and rainfall, soil moisture, temperature or photoperiod although growth was predominantly during spring and summer, which suggests that there is a relatively high temperature and photoperiod requirement for growth. But there may be lag periods and combinations of environmental factors involved, as reported for the initiation of growth in several chaparral species (Kummerow et al. 1981, Nilsen and Muller 1981). The determination of such complex environmental effects requires a more detailed, quantitative analysis of the seasonality of shoot growth linked with controlled-environment growth experiments.

There was no clear overstorey in these five year old communities, species such as M. muricata, S. radiata, L. parile and L. lanigerum occurred as emergents. But the growth of these species during spring and/or summer does not correspond to the spring or late spring-summer growth observed in overstorey species in other mediterranean shrubland or heathland communities respectively (Specht et al., 1983). The continued growth of mid- or ground-stratum species, such as S. distachya, G. plumosa, R. monanthus and B. abrotanoides, during summer also contrasts with the predicted spring or autumn period (Specht et al., 1983). The lower incidence of summer growth in south western Cape fynbos overstorey species, by comparison with southern Australian species, has been related to the high evaporation associated with the prevailing south easterly wind (Nieman, 1982) during summer in the Cape (Specht and Moll, 1983). But it is inappropriate to attempt to apply this understorey-overstorey growth season dichotomy to immature communities without clear stratification. P. burchellii is structurally an understorey species in the five year old Hutton community but it does form a distinct overstorey in some older communities (Boucher and Shepherd, in prep.). The shift in its growth season from 1980 to 1981-'82 suggests that growth could occur later, predominantly during summer, in older overstorey plants once the root system had become even more extensive and/or nutrients became more limiting (Christensen and Muller 1975, Rundel and Parsons 1980 cf Schlesinger et al. 1982).

Thus far available data do not provide conclusive evidence of direct links between seasonal availability of nutrients in both the soil and the plant and late spring to summer growth (Specht et al., 1983). A spring peak in resin-extractable phosphorus (a measure of "plant-available" phosphorus) was observed in the upper 40 cm of the Clovelly soil (Brown et al., in press). This peak may be attributed to microbial mineralisation of organic soil phosphorus (Brown, 1982). Neither litter decomposition rates (D.T. Mitchell, pers. comm.) nor soil nitrogen (W.D. Stock, pers. comm.) exhibited any obvious seasonality at Pella. Investigations of the seasonal levels of phosphorus in L. parile and of nitrogen in T. punctatus show that seeds and developing culms, shoots, leaves and inflorescences are nutrient "sinks" (S. Jongens-Roberts, W.D. Stock, pers. comm.). Nutrient levels decrease with leaf, stem and culm age suggesting that internal cycling of nutrients does occur. However the samples were not frequent enough to determine whether there was a dramatic withdrawal of nutrients from old leaves prior to litter fall which could initiate growth (cf Specht et al., 1983). The timing of litter fall appeared to be independent of the timing of shoot growth, occurring relatively synchronously, predominantly between November and February, in all species.

CONCLUSIONS

The results of this investigation do not show whether growth season in these eleven coastal fynbos species is determined by the seasonal-availability of nutrients (Specht et al., 1983), climatic factors (Adams and Radosevich 1978, Montenegro et al. 1979, Kummerow et al. 1981, Nilsen and Muller 1981, Specht 1981), inherited endogenous rhythms (Hanes 1965, Pierce, in prep.) or past climate (Specht and Rayson 1957, Levyns 1964). They do suggest that root depth and extent (T. punctatus cf S. distachya, L. parile cf L. lanigerum), soil moisture-holding capacity (L. parile on the Hutton and Clovelly soils during 1980-'81), plant water-use efficiency (D. proteoides cf L. lanigerum) and plant age (P. burchellii, G. plumosa and R. monanthus) affect growth season. But it must be borne in mind that "Perhaps the most critical caveat is one that must be observed in all studies dealing with pattern: the inability to make mechanistic or causal inference" (Rabinowitz et al. 1981). More detailed investigations both in the field and under controlled-environment conditions are necessary to determine causal mechanisms (cf Monasterio and Sarmiento, 1976).

ACKNOWLEDGEMENTS

I would like to acknowledge the supervision and support of Prof. E. J. Moll, the financial support of the CSIR Fynbos Biome Project, the advice of Prof. L. G. Underhill and P.R. Hurly on statistical and computer techniques and the co-operation of those who gave me access to their unpublished data.

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APPENDIX

TABLE 2 Results of Mann-Whitney and Kruskall-Wallis tests on T. punctatus monthly culm elongation data from the Hutton, Clovelly and Westleigh soils. Data are the test statistics of both tests.

		All 3 soils	HUTTON cf CLOVELLY	HUTTON cf WESTLEIGH	CLOVELLY cf WESTLEIGH
1980	Aug	0,0288*	0,0448*	0,2218	0,0185*
	Sept	0,0711	0,0083**	0,3795	0,2232
	Oct	0,7727	0,8619	0,5233	0,5649
	Nov	0,4651	0,1680	0,9610	0,5237
	Dec	0,5813	0,6381	0,4406	0,3308
1981	Jan	0,3560	0,2411	0,8805	0,1936
	Feb	0,4345	0,4148	0,2322	0,6003
	Mar	0,2918	0,4732	0,4906	0,0730
	Apr	0,9920	1,0000	0,8831	0,9515
	July	0,0751	0,1469	0,0391*	0,2656
	Aug	0,1677	0,2506	0,0485*	0,9161
	Sept	0,5142	0,6019	0,3424	0,3545
	Oct	0,0202	0,0228*	0,9293	0,0094**
	Nov	0,0043	0,4008	0,0115*	0,0027**
	Dec	0,0257	0,0713	0,1965	0,0155*
1982	Jan	0,1584	0,1821	0,0613	0,9463
	Feb	0,4793	0,7286	0,2323	0,4032

* indicates significant difference at the 5% level

** indicates significant difference at the 1% level

TABLE 3 Results of Mann-Whitney and Kruskall-Wallis tests on L. parile monthly shoot elongation data from the Hutton, Clovelly and Westleigh soils. Data are the test statistics of both tests.

		All 3 soils	HUTTON cf CLOVELLY	HUTTON cf WESTLEIGH	CLOVELLY cf WESTLEIGH
1980	June	0,1483	0,1676	0,3001	0,0774
	July	0,3264	0,2479	0,5434	0,1596
	Aug	0,9498	0,7224	0,8962	0,9471
	Sept	0,0226*	0,0191*	0,0351*	0,8118
	Oct	0,0002**	0,0004**	0,0032*	0,2690
	Nov	0,0048**	0,0024**	0,1648	0,0275*
	Dec	0,3136	0,9157	0,1071	0,4269
1981	Jan	0,0517	0,0164*	0,1342	0,6715
	Feb	0,8680	0,5459	0,8335	0,9155
	Mar	0,0682	0,0445*	0,0827	0,5232
	Apr	0,5610	0,3669	0,9455	0,2933
	May	0,0193*	0,0065**	0,0742	0,2846
	June	0,0868	0,5518	0,0477*	0,0961
	July	0,0869	0,0764	0,0523	0,6945
	Aug	0,3915	0,2737	0,2240	0,8825
	Sept	0,5695	0,3733	0,9696	0,3249
	Oct	0,1968	0,3494	0,8489	0,0356*
	Nov	0,8167	0,6888	0,9096	0,4763
	Dec	0,9786	0,9509	0,9738	0,7582
1982	Jan	0,4818	0,3715	0,8692	0,2418
	Feb	0,5808	0,5971	0,7335	0,2750

* indicates significant difference at the 5% level

** indicates significant difference at the 1% level

TABLE 4 Mean and standard error of 50 measurements (in cm.) of the height and North-South and East-West diameters of L. parile canopies on the Clovelly, Westleigh and Hutton soils

SOIL FORM	YEAR	HEIGHT	N-S DIAMETER	E-W DIAMETER
CLOVELLY	1981	78.7 ± 1.6	99.0 ± 4.2	95.8 ± 4.2
WESTLEIGH	1981	90.7 ± 2.1	113.9 ± 5.1	111.7 ± 5.1
CLOVELLY	1982	87.5 ± 2.3	102.3 ± 4.4	101.1 ± 4.5
HUTTON	1982	72.1 ± 1.7	58.8 ± 2.6	58.3 ± 2.4

REPRODUCTIVE PHENOLOGY OF NINE COASTAL FYNBOS SPECIES

J. E. M. Sommerville

SUMMARY

The reproductive phenology of nine south western Cape coastal fynbos species, representing the characteristic restioid, proteoid and ericoid components, was investigated from June 1980 to March 1982. The abundance of flowering activity during winter-spring suggests that the flowering of these species may have lower temperature and photoperiod requirements and higher soil moisture requirements than the predominantly spring flowering species in other mediterranean communities. The influence of such biotic factors as pollinators, dispersers, predators and competitors needs further investigation. Reproductive activity appears to have no effect on the season or quantity of the growth of individual shoots of these species.

REPRODUCTIVE PHENOLOGY OF NINE COASTAL FYNBOS SPECIES

AIMS

The broad aim of this study was to investigate the reproductive phenology of several coastal fynbos species and more specifically to attempt to answer the following questions:

1) How does the reproductive phenology of these coastal fynbos species compare with that of species in other fynbos and mediterranean communities?

2) Do taxonomically or structurally similar species exhibit similar seasonal reproductive patterns?

3) What, if any, is the relationship between the timing of flowering and shoot or culm growth?

4) Does flowering affect the growth of individual shoots or culms during the current and/or subsequent year?

STUDY AREAS

The study areas were at Pella, the CSIR Fynbos Biome Project's coastal fynbos intensive study site, located 35 km NE of Cape Town at 33° 31' S 18° 32.5' E. The vegetation is dominated by evergreen, sclerophyllous species representing the three characteristic fynbos elements: the proteoid, ericoid and restioid (Taylor 1978, Kruger 1979). The three study areas were situated in five year old Leucospermum parile - Stoebe leucocephala, L. parile - Thamnocortus punctatus and Diastella proteoides - Berzelia abrotanoides communities (Boucher and Shepherd, in prep.).

The soils at Pella are aeolian sands, a catena of five freely-draining soil forms exists, with two seasonally-waterlogged soils completing the seven major forms (M. Fry, pers. comm.). The communities investigated were on Hutton, Clovelly and Westleigh soils, respectively (MacVicar et al., 1977).

Climate data collected at the Pella climate station, Burgherspost farm (33° 30' S 18° 32' E) and the ATS weather station at Philadelphia (33° 40' S 18° 35' E) during the study period are illustrated in Figures 1 and 2.

METHODS

Common species representing the restioid, proteoid and ericoid components were investigated at each area, nine species in all, as shown in Table 1.

Table 1 Species investigated on the Hutton, Clovelly and Westleigh soils

	HUTTON	CLOVELLY	WESTLEIGH
RESTIOID SPECIES			
Thamnocortus punctatus Pillans Fam. Restionaceae	X	X	X
Staberoha distachya (Rottb.) Kunth Fam: Restionaceae		X	X
PROTEOID SPECIES			
Leucospermum parile (Salisb. ex. Knight) Sweet Fam. Proteaceae	X	X	X
Leucadendron lanigerum Buek ex Meisn. var. lanigerum Fam. Proteaceae	X		
Diastella proteoides (L.) Druce Fam. Proteaceae			X
ERICOID SPECIES			
Metalasia muricata (L.) D. Don Fam. Asteraceae		X	X
Staavia radiata (L.) Dahlg Fam. Bruniaceae	X		
Berzelia abrotanoides (L.) Brongn Fam. Bruniaceae			X
Griseb. achia plumosa Klotzsch subsp. plumosa Fam. Ericaceae		X	

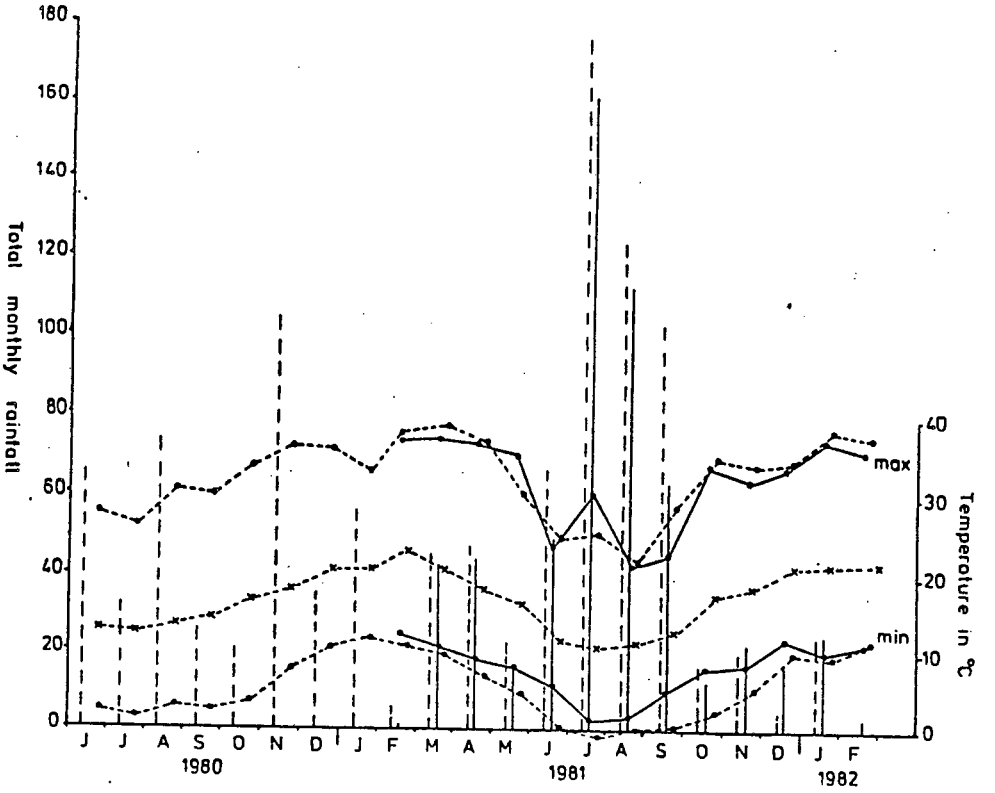

Figure 1 Monthly rainfall and temperature data from June 1980-February 1982. Total monthly rainfall from the Pella climate station (|) and Burgherspost farm (¦). Absolute monthly maximum (●——●) and minimum (●——●) air temperatures from the Pella climate station and maximum (●– – –●), minimum (●– – –●) and average (×– – –×) temperatures from the Philadelphia weather station.

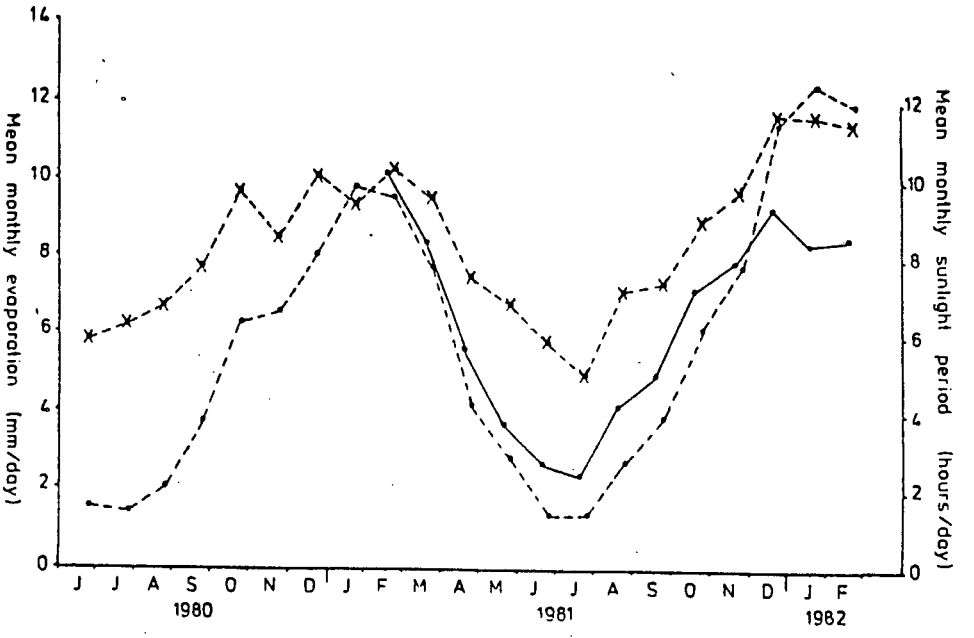

Figure 2 Average monthly A-pan evaporation from the Pella climate station (●——●) and Philadelphia weather station (●– – –●), from June 1980 to February 1982. Average monthly sunlight hours (–X–) from the Philadelphia weather station, from June 1980 to February 1982.

Two shoots, or restioid culms, were labelled on each of ten plants of each species at the three sites. Observations of the reproductive activity of the labelled plants and individual shoots or culms were recorded at approximately monthly intervals from June 1980 to March 1982. These data were supplemented by data from litter collected in two, 15 cm-diameter pots under an individual or group of individuals of each species at the three sites.

RESULTS

Data from the labelled plants and shoots, and from the litter samples have been combined and illustrated by bar graphs representing the periods during which bud set, flowering and fruit or seed fall occurred. Bar graphs representing shoot or culm growth periods have been included (Sommerville, in prep.).

Restioid species

The reproductive phenology of both male and female T. punctatus plants was similar on all three soils (Figure 3). The first terminal inflorescence buds were distinguishable during November and anthesis occurred four months later, during March. Seed fall occurred during the period from March-April to July-August, up to five months after anthesis.

Terminal inflorescence buds were observed on S. distachya from February to June on the Clovelly soil and from January to July on the Westleigh (Figure 3). Anthesis was not conspicuous but appeared to occur during July to August on the Clovelly soil and June to August on the Westleigh. Seed fall was recorded from August to December and during May on the Clovelly soil, and during September and October on the Westleigh. Although culm growth occurred throughout the year on the plant as a whole, inflorescences developed after the growth of individual culms. The growth of fertile and vegetative culms was comparable.

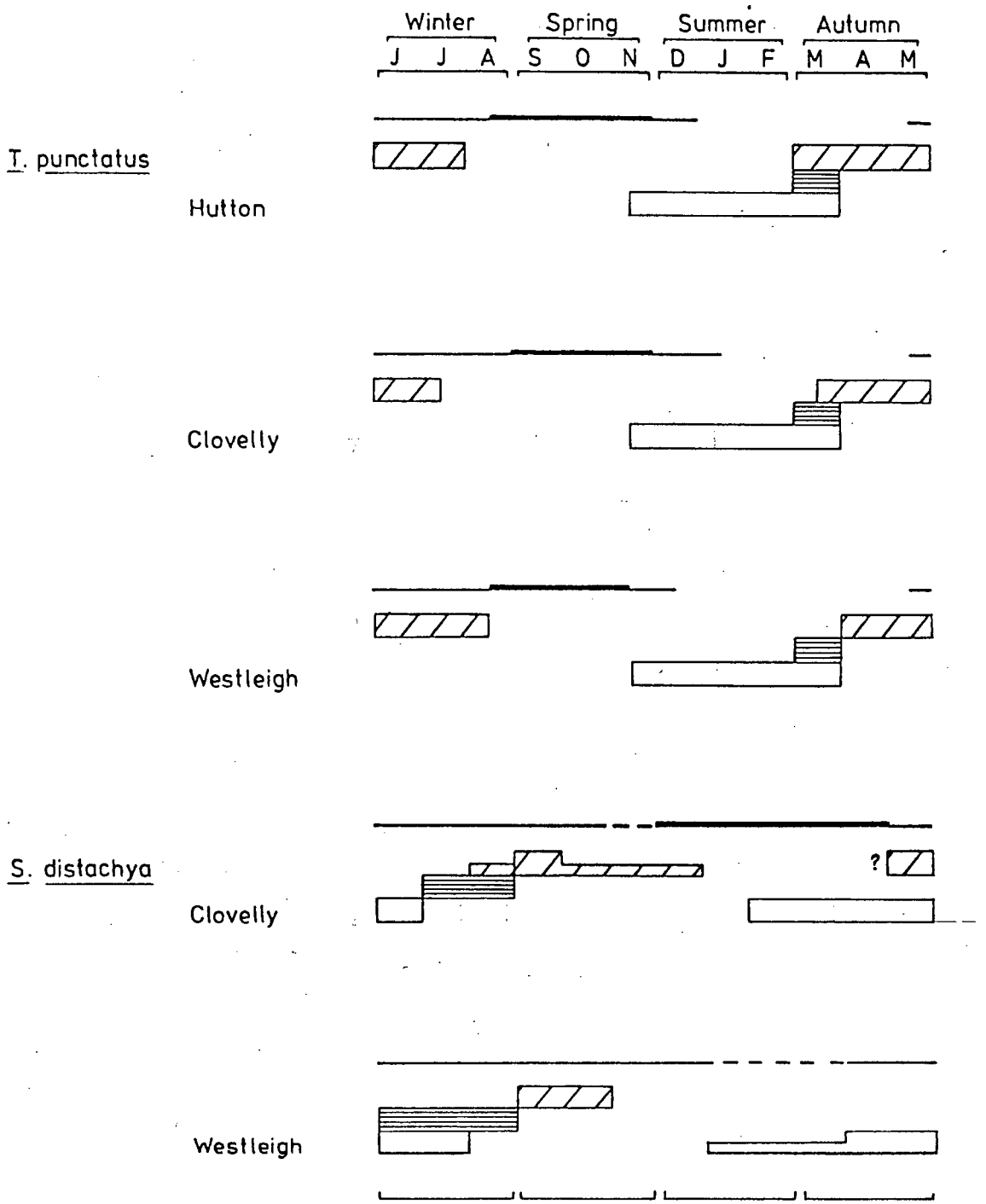

Figure 3 Reproductive phenograms and growth of restioid species: T. punctatus and S. distachya

inflorescence buds, anthesis, seed fall

culm growth ——, maximum growth ▬▬, minimum growth — — —.

Proteoid species

Axillary flower buds were observed on L. parile from May to December-January on all three soils (Figure 4). Flowering occurred from August-September to January on the Clovelly and Westleigh soils. Only three of the ten labelled plants on the Hutton soil flowered during 1980, and five during 1981, as a result the flowering period was shorter on this soil. There was no obvious effect of flowering on the growth of individual shoots, on some shoots both activities occurred two years in succession, together or singly (Table 2). Seed fall was recorded from November-December to January-February on the Hutton and Clovelly soils and from October-November to January-February on the larger plants on the Westleigh soil (Sommerville, in prep.).

Terminal, male flower buds were observed on L. lanigerum plants from July-August to September (Figure 4). The development of the female cones prior to flowering was hidden by the terminal leaves. Flowering of both sexes occurred from June-July to September-October. Again there was no obvious relationship between flowering and the growth of individual shoots (Table 2). Female cones are retained on the plant and contrary to Williams' observation (1972) that seed is only released after fire, winged seeds were recorded in the litter during February 1982.

Terminal flower buds were observed on D. proteoides from July-August to March, and flowers throughout the year, except during June (Figure 4). Buds developed into flowers over a period of less than one month to three months. Flowering and growth appeared to be relatively independent of one another in terms of their occurrence both seasonally and from year to year (Table 2). Few fruits were produced during February 1982, in comparison with the abundance of flowers.

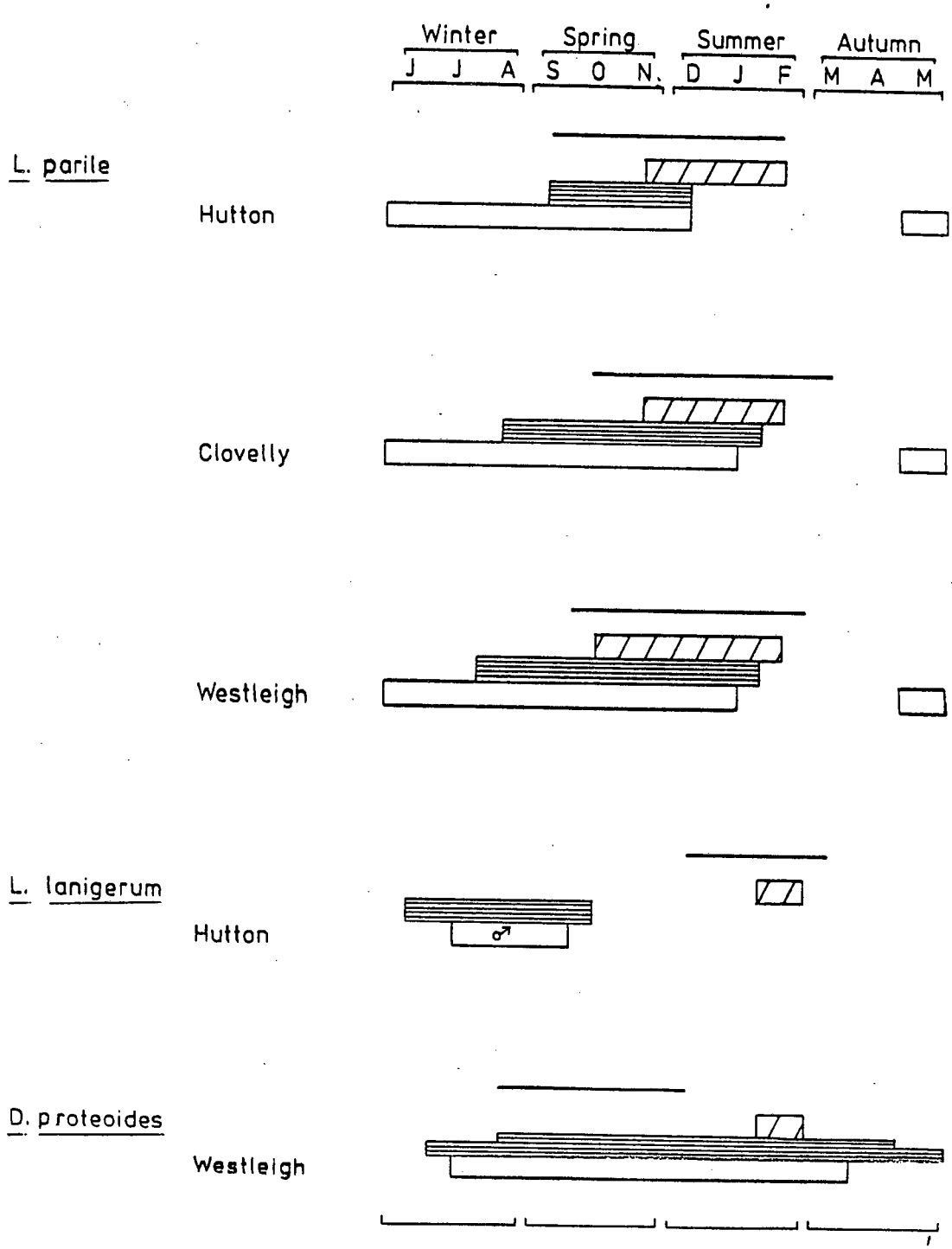

Figure 4 Reproductive phenograms and growth of proteoid species: L. parile, L. lanigerum and D. proteoides

flower buds, flowers, seed fall, —— shoot grow

Table 2 Activity of labelled proteoid shoots during two successive years

Shoot activity		Number of labelled shoots				
		L.parile			L.lanigerum	D.proteoides
1980-'81	1981-'82	Hutton	Clovelly	Westleigh	Hutton	Westleigh
Flower+grow	Flower+grow	1	1	5	2	5
Flower+grow	- grow	-	1	-	-	2
Flower+grow	Flower -	-	-	-	1	-
Flower -	Flower+grow	-	-	-	-	-
Flower -	Flower -	-	-	-	-	1
Flower -	- grow	-	-	-	-	2
- grow	Flower+grow	3	1	2	1	-
- grow	- grow	8	3	1	1	1
- grow	Flower -	-	-	-	-	-
Flower -	- -	-	-	-	5	2
- grow	- -	3	1	1	1	-
- -	Flower -	1	-	-	-	2
- -	- grow	1	6	4	-	-
- -	- -	3	7	7	9	5

Ericoid species

The reproductive phenology of M. muricata was similar on the Clovelly and Westleigh soils (Figure 5). Flower buds were observed from February-March to June and flowering occurred almost exclusively during June. Seed fall followed during July to September-October. There was little overlap between growth and reproductive activity and both occurred together or singly, two years in succession on some shoots.

S. radiata flower buds occurred predominantly from March to October and flowers almost throughout the year, with a minimum between December and February (Figure 5). Some shoots both grew and flowered and others grew or flowered during one year, some shoots grew and others flowered two years in succession. Seed fall occurred from June to November-December.

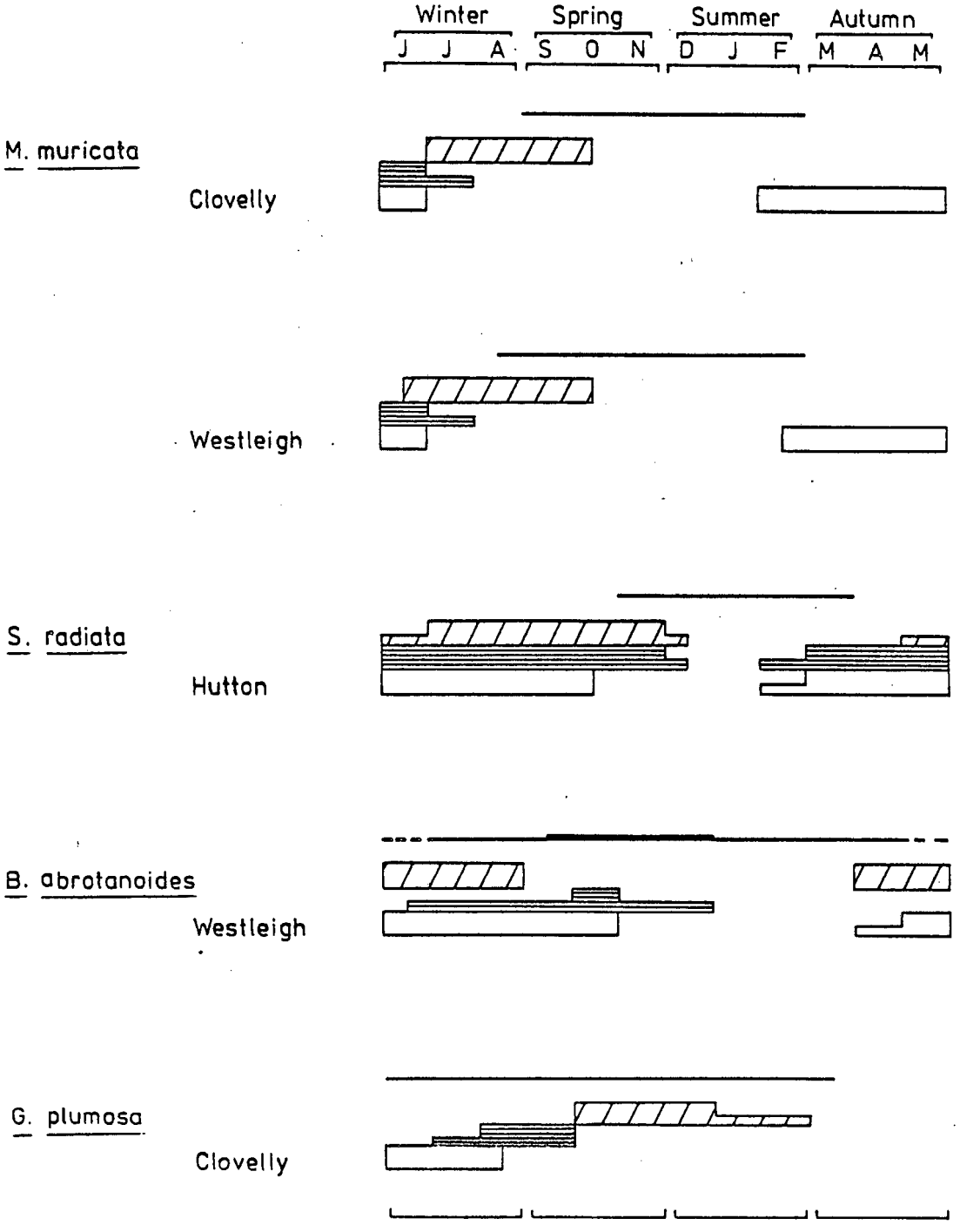

Figure 5 Reproductive phenograms and growth of ericoid species: M. muricata, S. radiata, B. abrotanoides and G. plumosa

flower buds, flowers, fruit or seed fall

shoot growth ——, maximum growth ▬▬, minimum growth — — .

B. abrotanoides flower buds were observed from April to October when both peak flowering and growth occurred (Figure 5). Only three labelled shoots produced flowers; one grew extensively during 1980-'81 and grew and flowered during 1981-'82, two grew and flowered during 1980-'81 and were inactive during 1981-'82. Fruit fall occurred from April to August.

G. plumosa produced flower buds from June to July-August and flowers from July to September (Figure 5). A single shoot labelled through two seasons, flowered during both. Dead flowers, which were assumed to bear seed, fell during October-November 1980 and from November to February 1981-'82.

DISCUSSION

Comparisons with other data

The data show that flowering in these nine coastal fynbos species is spread throughout the year with most flowering activity occurring during the winter-spring period, June to November. This is similar to the flowering peak observed in another coastal fynbos community (Sommerville in Siegfried, 1982) but earlier than the spring or spring-summer peak observed in south western Cape mountain fynbos, southern Australian heath, Californian chaparral and Chilean matorral (Rycroft 1950, Groves and Specht 1965, Hoffmann et al. 1977)

The two restioid species investigated flowered during autumn, March, and winter, June to August. But a synthesis of available fynbos phenology data (Pierce, in prep.) shows that flowering in the Restionaceae is not generally confined to autumn-winter, or to summer as observed in southern Australian heath (Groves and Specht, 1965).

L. parile and L. lanigerum flowered during spring-summer and winter to early spring, respectively, conforming with other winter-rainfall species in their genera (Rourke 1972, Williams 1972) and earlier than the southern Australian Proteaceae which "tend to flower during summer" (Groves and Specht, 1965). Flowering in D. proteoides extended beyond the spring-summer period of many proteoid species, conflicting with the observation that flowering in proteoid species is more seasonal in the south western Cape than in the south and south eastern Cape (Pierce, in prep.) This may be related to the fact that most of the species on which this observation was based were large-leaved,

large-flowered over- or mid-storey species while D. proteoides is a mid- to dwarf-understorey species (Boucher and Shepherd, in prep.) with small leaves and flowers. It is interesting that seed fall in the three proteoid species occurred during spring and summer although L. parile and D. proteoides have ant-dispersed and L. lanigerum wind-dispersed seeds (Williams 1972, Bond and Slingsby 1983).

Flowering and fruit or seed fall in the ericoid species occurred predominantly during winter-spring, although it is a structurally and taxonomically heterogeneous group. The observed flowering of G. plumosa during winter and early spring is earlier than the summer-autumn period which includes many other fynbos Ericaceae (Pierce, in prep.) or the spring period in the southern Australian equivalent: the Epacridaceae (Groves and Specht, 1965).

Relationship between flowering and growth

Flowering often follows shoot growth in the dominant trees and shrubs and precedes growth in understorey or subdominant species in southern Australian heath (Specht, 1981). There were no true dominant,overstorey species in the communities studied at Pella, however, there were emergent species, including M. muricata, L. parile and L. lanigerum. Flowering occurred midway between two shoot growth seasons in M. muricata, preceded growth in L. lanigerum and preceded or coincided with growth in L. parile. The relationship between the timing of shoot growth and flowering in the species investigated appears to be related more to the duration of shoot growth and of flowering and to plant morphology, than to species dominance or stratification. For example S. distachya, B. abrotanoides and G. plumosa flower during their extended growth periods. D. proteoides, on the other hand, has an extended flowering period so that flowering occurs before, during and after shoot growth. T. punctatus produces a single cohort of fertile culms each year and since inflorescences are terminal flowering occurs after growth (cf Jow et al., 1980).

The timing of shoot growth relative to reproductive activity may also be related to temporal partitioning of limited resources within the plant. Mooney (1983) states that the growth of different plant parts, such as roots and stems, is generally asynchronous and attributes this in part to the "limitation of building materials". Similarly one

might predict a temporal separation of reproductive and vegetative development, as observed in female plants of a Chilean tree species (Hoffmann, 1981). The observed synchrony in shoot growth and reproductive activity in L. parile is in complete contrast to this prediction. There was a tendency to temporal separation in T. punctatus, M. muricata and L. lanigerum. But, this may also be attributed to plant morphology in the case of T. punctatus and to different environmental requirements for flowering and growth in M. muricata. There may be considerable temporal overlap in resource allocation to vegetative and reproductive organs in L. lanigerum because of the developing and maintenance of the female cone prior to flower and seed dispersal respectively.

Thus it appears that the resources necessary for vegetative and reproductive development in these species are not sufficiently limited to prevent synchronous activity. This is further supported by the fact that flowering had no obvious effect on either the timing or quantity of the growth of individual shoots or culms. Sterile shoots or culms grew comparably to fertile shoots or culms in all species. In addition the growth of culms or shoots on female plants of T. punctatus and L. lanigerum did not appear to be affected by the "energetic cost" of fruit development (cf Hoffmann, 1981). The observed alternation of flowering and shoot growth from year to year, on female plants of the Chilean species (Hoffmann, 1981) did not occur on labelled shoots of the ericoid or proteoid species investigated.

Factors affecting reproductive phenology

The initiation of spring flowering in four chaparral species appears to be controlled by "warming hours" ($\geq 15^{\circ}C$) accumulated after soil moisture has reached a certain threshold ($0.1 g ml^{-1}$) during the previous autumn (Kummerow et al., 1981). Species such as M. muricata and S. distachya, which flowered predominantly during winter may have lower temperature and photoperiod (Nilsen and Muller, 1981) and higher soil moisture requirements for flower initiation. T. punctatus on the other hand, flowered during March, at the end of summer, suggesting that flowering may have a greater "warming hours" requirement than spring flowering species. The lower incidence of flowering in L. parile on the Hutton soil suggests that this species has a soil moisture requirement for flowering. The Hutton soil appears to contain low levels of plant-available moisture as a result of its high water-holding capacity (Sommerville, in prep.), which may limit flowering. Reproductive success in the chaparral species Arctostaphylos viscida is also reduced under drought conditions by a reduction in the

number of flower primordia formed (Parsons et al., 1981). By comparison species such as S. radiata and D. proteoides, which flower almost throughout the year, obviously have broad environmental tolerances.

Fruit or seed dispersal occurred several months after flowering in most species but six to seven months later in B. abrotanoides and more than 12 in L. lanigerum. Because the fruit of different species ripened at different rates fruit fall was more evenly spread over the year than flowering. Both flowering and fruiting time are probably affected by biological factors such as pollinators, dispersers and predators. "An evolutionary commitment to dispersal (or pollination) via one group of animals over another (may carry) carries with it a phenological commitment to the timing of fruit ripening or seed release (or flowering)" (Thompson, 1981 - my inclusions in brackets). The effects of these climatic and biological factors which probably involve lag periods and combined effects, as well as others such as endogenous rhythms (Pierce, in prep.) and competition (Stiles, 1977) need to be investigated further and experimentally determined (cf Monasterio and Sarmiento, 1976).

CONCLUSIONS

1) Comparisons with mountain fynbos and other mediterranean communities show that there is more flowering activity during winter among these coastal fynbos species.

2) Flowering in the two restioid species was confined to autumn-winter, seed fall was more extended, occurring during autumn to spring.
The flowering of the three proteoid species occurred at various times throughout the year. Seed fall was relatively synchronous during summer, in spite of differences in their seed dispersers.
Both flowering and fruit fall in the four ericoid species occurred predominantly during winter-spring.

3) The timing of flowering relative to shoot or culm growth could be related to the duration of both and to culm morphology in some species.

4) Flowering and shoot growth may occur together or singly during successive years on individual shoots of the three proteoid species, M. muricata and S. radiata.

5) Causal mechanisms of flowering and fruiting need to be investigated by experiments on the effects of such environmental factors as temperature, moisture and photoperiod, singly and in combination, and by investigations of the seasonal relationships between co-occurring species and their pollinators, dispersers and predators.

ACKNOWLEDGEMENTS

I would like to acknowledge Prof. E. J. Moll for his supervision and support and the CSIR Fynbos Biome Project for funding this research.

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CONCLUSIONS

The specific conclusions of each paper have been dealt with at the end of each paper. What remains is to draw general conclusions from this research as a whole. Summer growth is discussed in relation to water stress, nutrient availability and plant characters such as age and root depth.

The data show that growth in these coastal fynbos species is most common during both spring and summer, only L. lanigerum is essentially a summer growing species. The lower incidence of late spring-summer growth in Cape fynbos species, by comparison with southern Australian heath, has been attributed to the higher levels of evaporation in the Cape as a result of stronger winds, particularly during summer (Specht and Moll, 1983). In addition, direct comparisons cannot be made with the predictions of Specht et al. (1983) for over- and under-storey species because these five year old communities lacked a true over-storey. But the observed change in the growth season of P. burchellii, which becomes a dominant overstorey species in some older communities, suggests that its growth season may occur during summer in older plants. This illustrates a shortcoming of the understorey-overstorey growth model in terms of these coastal fynbos communities; it does not explain the growth patterns of these early successional communities, which are common in this fire-prone mediterranean-type vegetation (Taylor 1978, Kruger 1979).

The xylem pressure potential data confirm that a species such as L. parile, which may continue shoot growth during summer, experiences low levels of water-stress during spring-summer. This is supported by an investigation of the seasonal water relations of several mountain fynbos species which "indicated little or no plant water stress" in most of the species investigated; "in spite of a more than twofold difference in annual precipitation" at the two sites (Miller et al., 1983). However the early growth season of the L. parile plants on the Hutton soil during 1980-'81 illustrates the variability in the growth season of a species as a result of variability in root extent, annual precipitation and soil moisture-holding capacity. It is not possible to determine which, if any, of the factors which appear to affect growth season is responsible for summer growth in some southern Australian heath and Cape fynbos species. Available data from nutrient studies at this coastal fynbos site do not provide conclusive evidence of the precise seasonality of nutrient-availability suggested by Specht et al. (1983). But the

considerable overlap observed between reproductive activity and shoot or culm growth suggest that nutrient or other resources are not limiting in these species (cf Mooney, 1983).

It seems that only those species with deep, or otherwise extensive root systems and probably low transpiration water losses efficiently utilise summer rainfall and/or stored moisture and are therefore able to grow during summer. The higher incidence of summer rainfall in both southern Australia and the Cape fynbos region by comparison with other mediterranean-type regions (Specht 1969, Cody and Mooney 1978, Kruger 1979) probably contributes to the incidence of summer growth (Specht, 1981). These summer growing species might have a competitive advantage in the overstorey of mature, more nutrient-limited (cf Christensen and Muller, 1975) communities if their growth period coincided with that of maximum nutrient-availability in both the plant and the soil, as Specht et al. (1983) suggest.

However the data, presented here, show that the reproductive and vegetative phenophases of these coastal fynbos species cannot be easily classified in terms of factors such as growth form, stratification, root depth or plant age. Rather they provide evidence of the "diverse phenologies" observed in mountain fynbos species "which, if phenology correlates with strategies of carbon gain and nutrient allocation, could be part of the means of maintaining community diversity in the face of seasonal drought, infertile soils and periodic fire" (Kruger, 1981).

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